Limits to Plant Regeneration in Alpine Vegetation on Tasmania's Central Plateau

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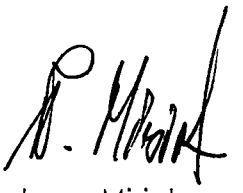

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Abstract

The long history of disturbance by human activities on Tasmania's Central Plateau has resulted in some of the most eroded alpine and subalpine country in Australia. Although the rate of vegetation and soil loss has declined following the introduction of myxomatosis, prohibition of burning, and the exclusion of stock grazing within the Tasmanian Wilderness World Heritage Area, recovery has been relatively slow, and erosion continues to occur. This study examined some of the current biotic and abiotic parameters affecting plant regeneration in alpine vegetation in the Central Plateau region.

Seed traps were used to assess the availability of seed for regeneration in different microhabitats. There were significant seasonal and locality differences in seed density and species richness. A total of 14 to 24 seed taxa per site were trapped over a 14 month period. Average seed densities per month ranged from 5 to 3,090 seeds m^{-2}. In general, bare microhabitats captured similar numbers of seeds and taxa to those trapped in existing vegetation clumps, at the edges of prostrate *Grevillea australis*, and directly underneath this shrub. Germination trials of a variety of species showed high germinability under wide temperature regimes, indicating the potential for recruitment throughout much of the year. In addition, pitfall trapping found little evidence of invertebrate taxa associated with post dispersal seed harvesting in the area, but potential predation by small mammals and birds cannot be excluded.

Some aspects of microclimate in eroded bare patches and under *G. australis* were also recorded. This native shrub species appears to play an important role in ameliorating the microenvironment for seedling establishment due to its prostrate habit, which limits levels of excessive solar radiation, velocity of desiccating wind gusts, and the extent of frost heave activity. Consequently, numbers of seedlings were significantly higher under *Grevillea* shrubs than in open patches throughout the year, despite seed arrival being similar. The frequency of freeze-thaw cycles, minimum soil surface temperature and relative humidity however, were not detectably different between open and *Grevillea*

microhabitats, while jute matting and *Orites acicularis* slash were effective in increasing minimum soil surface temperatures and relative humidity, and reducing freeze-thaw and frost heave activity compared to bare areas. Unexpected microclimatic readings could be attributed to the highly heterogeneous nature of the microhabitats.

This baseline data will improve our understanding of the processes and requirements for regeneration in highland areas and contribute to effective conservation and ecosystem management.

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Chapter 1. Introduction

INTRODUCTION

High elevation regions have been subject to a variety of anthropogenic disturbances worldwide, often with unparalleled impacts on vegetation and soil (Körner 1999). The diverse pressures applied to these areas have depended on, and have been tempered by, the suitability of the local conditions for exploitation, such as topography, accessibility, and climate. Some of the more common past and present land uses of highland regions include activities associated with recreation and tourism (especially skiing), mining, livestock grazing, and hydroelectricity generation. All these activities have been pursued in Australian alpine landscapes and have invariably resulted in degradation of the natural vegetation and soils affecting wildlife habitat and scenic appeal, but most notably water catchment values (Costin 1973). Currently, managing mountain catchments for high water yields and tourism is of primary importance, and maintenance of adequate vegetation cover is essential for those landscape uses.

Natural regeneration following disturbance in alpine areas is extremely slow, often recorded in terms of many decades (Bayfield *et al.* 1984; Bridle *et al.* 2001; Ebersole 2002). Although ample seedlings are present, mortality is high even in undisturbed systems (Chambers 1995a; Erschbamer *et al.* 2001). Körner's survey of the literature (Körner 1999) suggests that over a 12 month period, seedling mortalities regularly exceed 50% in large seeded species and 99% in small seeded species in alpine communities. Active restoration of damaged areas is often difficult and expensive or not feasible at all for large or inaccessible areas (Körner 1999). Restoration of the damage can be of limited success due to the severity of the environment. Recovery is impeded by a combination of low growing season temperatures, frost disturbance, desiccating

winds, and high radiation loads, which impact on the capacity of plants to produce seeds, germinate, establish, and grow.

The response of a community to disturbance will depend on the scale, timing, frequency and intensity of the disturbance, but also on the species present at the site (Chambers 1995a). Large disturbances that remove vegetation and soil could create conditions for revegetation comparable to those in primary succession – nutrients may be lost along with the seed bank or mycorrhizae, and a source of seed for new colonisers may be some distance away. In the absence of vegetatively propagating species, seed dispersal patterns are important. Species with small, easily dispersed seeds, or with seed characteristics conducive to wind dispersal would be more likely to arrive in gaps in the vegetation than large seeded, poorly dispersed species. Once seeds arrive in an area, they could be subject to predation by omnivorous or granivorous species of insects, birds, mammals or rodents, which can be locally abundant in some alpine systems (Chambers 1995a). The patterns of predation could in turn be influenced by existing vegetation and size of gaps, with different groups of species foraging preferentially in different microhabitats. Physical microhabitat characteristics such as soil particle size, surface and soil temperature, moisture, freeze-thaw activity and the light environment will therefore influence not only seed entrapment and seed survival, but also germination, seedling emergence and survival (Chambers & MacMahon 1994; Chambers 1995a; Jumpponen *et al.* 1999; Anisuzzaman *et al.* 2001). Hence, seed-seedling conflict can occur where conditions favourable to seed accretion and preservation will not necessarily be conducive to seedling establishment and growth (Chambers 1995b; Schupp 1995; Titus & del Moral 1998).

Revegetation can therefore be hindered by lack of seed input (Erschbamer *et al.* 2001), low rates of seed entrapment (Fort & Richards 1998), seed predation (DeSimone & Zedler 1999; Muñoz & Cavieres 2006; Orrock *et al.* 2006), or low seedling survival due to the lack of suitable conditions for establishment once seeds are deposited in a microsite (Erschbamer *et al.* 2001; Cooper *et al.* 2004). Naturally, recruitment for many species can be limited by a combination of seed and microsite availability (Eriksson &

Ehrlén 1992). In alpine and arctic environments, high seedling mortality has also been attributed to insufficient carbohydrate accumulation (Douglas 1995). On Tasmania's Central Plateau, a combination of soil loss, exposure to low temperatures, short growing season, frost heave, strong winds, and grazing pressure from both introduced and native herbivores, are thought to limit revegetation of degraded sites (Jackson 1973; Pemberton 1986; Cullen 1995; Bridle & Kirkpatrick 1999).

OBJECTIVES

The main objectives of this study were to gain insight into the biotic and abiotic limitations of natural regeneration in a highly degraded alpine system in Tasmania. The Central Plateau is a unique environment and information from alpine regions on mainland Australia or other parts of the world might not be adequate to understand the processes involved. Although the severe climatic conditions of the Central Plateau environment have often been discussed as playing a major role in preventing revegetation (Mitchell 1962; Pemberton 1986; Richley 1986), no quantitative data describing these limitations in such a structurally varied environment has been collected.

Essentially, the questions addressed in this thesis were:

- Are there microclimatic differences in the major microhabitats - in large bare gaps and under *Grevillea australis* canopies? How do microclimatic conditions in artificial microhabitats currently employed in geoconservation measures compare to those in natural sites? (Chapter 2)
- What are the seedling densities, do they change seasonally, and does their distribution show any patterns or vary with time? (Chapter 3)
- What is the seed rain of these communities? Does it vary seasonally? Are seeds deposited evenly in the different microhabitats and are seeds of all species distributed evenly among microhabitats? (Chapter 4)

- Are seeds, and therefore potential seedlings, removed from the community by invertebrate harvesters? Does the invertebrate fauna of the communities include many seed eating species? (Chapter 5)
- What are likely seed germination patterns of the community? Are many species ready germinators, and therefore likely colonisers, or are longer term seed banks more likely to be formed? Are there specific dormancy breaking cues for some species? (Chapter 6)
- How do all these various processes impact on revegetation of degraded sites on the Tasmanian Central Plateau? (Chapter 7)

Improving our understanding of the processes and requirements for regeneration in highland areas will contribute to effective ecosystem management for catchment conservation for water quality and storage, tourism and recreation, nature and landscape conservation, and aesthetic value.

The scope of this work covers diverse aspects of the overall regeneration story, rather than delving into particular areas of possible research concerning biological and physical processes. The conflict of short term research into a long term process can only ever give a snapshot of the current situation and ideally a longer term study would address seasonal variability affecting seed and seedling dynamics. One major piece of the puzzle is missing – the assessment of seed banks to give a complete picture of the regeneration process. However, this would be a large project in its own right, and all the other time intensive aspects of this study excluded a fair analysis of seed bank dynamics.

THE CENTRAL PLATEAU

The Central Plateau of Tasmania represents approximately 43 % of all alpine and sub-alpine country in Australia (Costin 1973), accounts for 7.4% of the island's total area, and contributes about 78% of Tasmania's high mountain environments (Shepherd *et al.* 1975). The region is well defined from the Travellers Range escarpment in the west, along the northern and eastern edges by the Great Western Tiers, to Table Mountain in the south-east, but to the south it slopes gently and the 600 m contour was taken as a convenient boundary by Banks (1973). Altitude reaches up to 1499 m a.s.l. in the northwest (King David's Peak at the Walls of Jerusalem), but is generally a gently undulating area (Cullen 1995) (Figure 1.1). It is a glaciated landscape with thousands of lakes – over 4 000 in 10 000 square kilometres (Banks 1973), and is an important water catchment area.

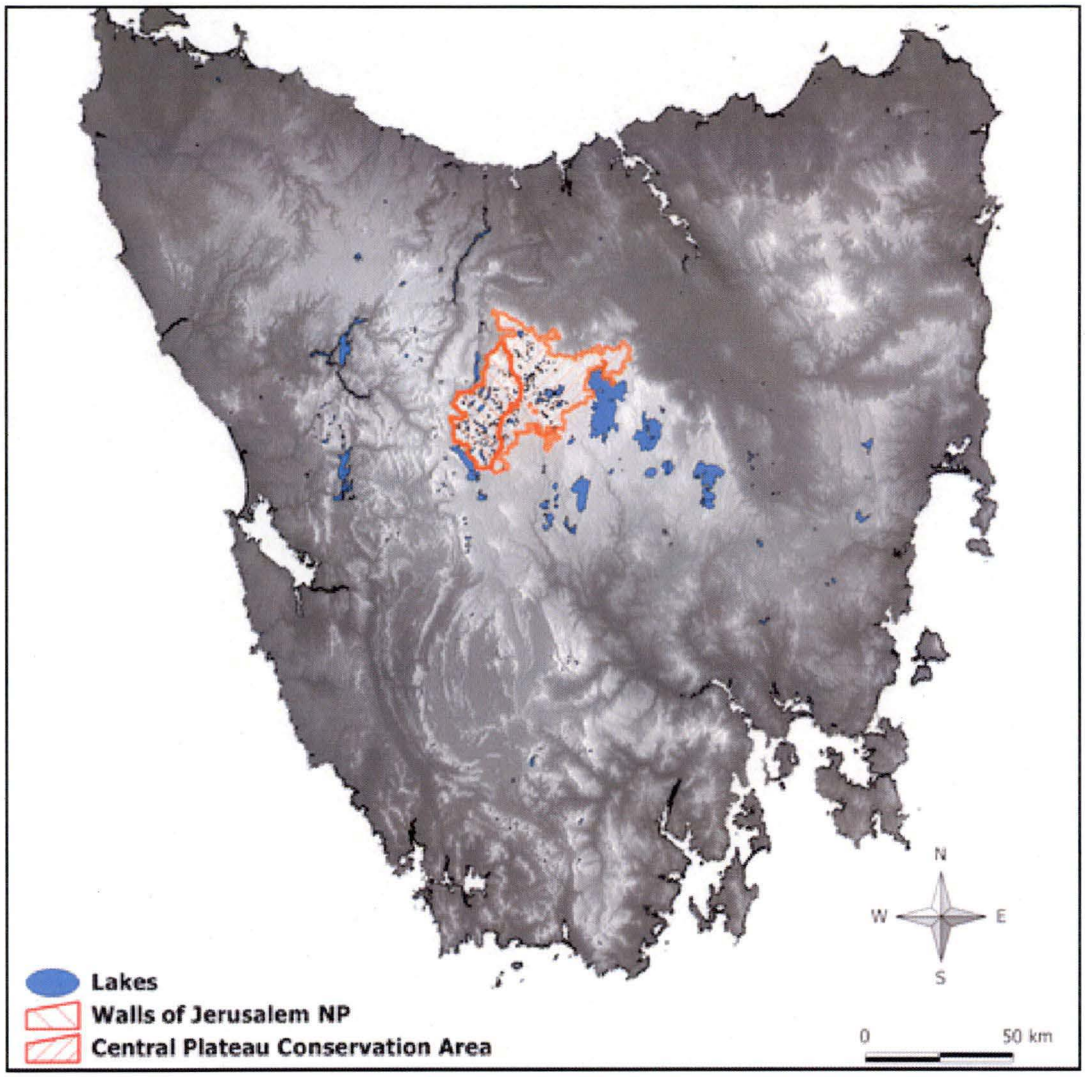


Figure 1.1 Tasmania with Central Plateau World Heritage Area Boundaries. Lighter areas indicate higher elevation, dark grey lower elevation.

Past history

In parallel with alpine regions of mainland Australia (Mitchell 1962; Clothier & Condon 1968; Bryant 1969), the Central Plateau has a long history of disturbance by human activity from fire, grazing, infestation by rabbits, leisure activities such as 4 wheel driving and horse riding, as well as road and dam works associated with hydro-electricity activities. Consequently, vegetation over large areas has been modified,

particularly as a result of burning and grazing (Figure 1.2). Although the Central Plateau Protected Area was reserved in 1978 under the Crown Lands Act (The Lands Department 1982) and World Heritage status was conferred on about two thirds of the Plateau in 1982, with minor additions in 1989 (Corbett 1996), the area contains some of the most eroded alpine and sub-alpine country in Australia (Mitchell 1962; Cullen 1995).

Figure 1.2 Severe sheet erosion on Liawenee Moor, west of Great Lake.

Prior to European settlement, Aborigines of the Big River tribe occupied the Central Plateau during the warmer months of the year, burning bushland to promote grassy areas which facilitated hunting wallabies (Shepherd 1973). The first official lease of 1100 acres fronting the western side of the Ouse River at Liawenee was granted to Richard Pybus in 1840, but parts of the area around Great Lake were already stocked with cattle by 1825 (The Lands Department 1982; Crawford et al 1962 in Cullen 1995). By c.1860, most of the better land on the Plateau had been selected, with stocking rates relatively high (The Lands Department 1982). Overstocking was often deliberate to produce "hunger fine" wool (Shepherd 1973; Jetson 1989). Pastures and water supplies on lowland properties were often exhausted by the end of December, but in the highlands the growing season does not begin until about November, with green feed and plentiful water usually available throughout the summer. Stock were sent to the "Lake Country" during December and January and returned to lowland properties in April and May. In addition, small flocks of sheep were wintered in the more favourable areas (Shepherd 1973).

Fire has been used extensively as a pasture management technique to remove fibrous and woody growth and stimulate "a green pick" for stock. This practice depleted the tussock grass reserves and resulted in subsequent death of the plants. This was further compounded by overgrazing by rabbits, which appeared on the plateau around 1910 and reached plague proportions during the 1920s to early 1950s (Jackson 1973). Cullen (1995) suggested the grazing and regular burning regime created a suitable habitat for rabbits on the Plateau and promoted the large numbers of this herbivore. Practices associated with grazing together with rabbit infestation reduced the carrying capacity of the Plateau by at least 40% (Shepherd 1973).

According to Mitchell (1971), fire has been the main initiator of erosion on the Central Plateau. Out of control fires have caused widespread and severe damage. The intense fires of 1960-61 were especially damaging, with the resulting loss of vegetation leaving the soil exposed to erosion. Following the fires, Mitchell (1962) reported more than one third of the plains west of Great Lake denuded of vegetation, and soil removed to a

depth of 30 cm in some instances. A decade later, in the same area, Bryant (1971b) reported 40-50% bare ground was common. Richley (1986) recorded 37% bare ground in the most damaged area subjected to past grazing, with another 13% bare ground covered by prostrate shrubs, while some eastern areas were observed to have less than 50% vegetation cover (Pemberton 1986). Despite early reports on the enormous degree of land degradation (Mitchell 1962; Colclough 1970; Mitchell 1971; Shepherd 1973; Shepherd *et al.* 1975; Pemberton 1986; Richley 1986), grazing leases were not revoked until 1989.

The economic value of the Plateau now lies it its status as a major water catchment for hydroelectricity generation. Use of water resources for hydroelectric purposes began in 1911 with the exploration of the waters of the Great Lake catchment (Shepherd 1973). Water management is closely tied to vegetation management. Vegetation plays an important role in intercepting small water droplets and controls infiltration of rainwater into the ground. Vegetation cover is also essential in preventing sedimentation of lakes and tarns and hence preserving water quality on the Plateau (Edwards 1973).

Following the introduction of myxomatosis in 1952/1953 and the prohibition of burning and exclusion of stock grazing in 1989 within the Tasmanian Wilderness WHA, the rate of vegetation and soil loss declined (Cullen 1995). Removal of domestic stock is most likely the major cause of current recovery (Bridle 1987). However, recovery is relatively slow and uneven with grassland responding better to grazing exclusions than heath (Bridle 1987). Revegetation of bare ground averaged 1% per year over 5 to 23 years across several sites on the Eastern Plateau (Bridle & Kirkpatrick 1999; Bridle *et al.* 2001). Severely eroded areas revegetate much more slowly and continue to erode in some cases (Bridle 1987). Major soil loss in the form of sheet erosion has already taken place, preventing plant re-establishment. Following intense or repeated fires, wind and water have removed the O and A soil horizons, resulting in extensive erosion up to 50 cm deep (Figure 1.3), leaving the rocky pavement of the B horizon (Cullen 1995). Within the World Heritage Area of the Plateau, Cullen (1995) reported 11 035 ha to be

in a degraded state, with c. 161 ha exceeding 70% bare ground and c. 2 990 ha with between 40 and 70% bare ground.

Figure 1.3 Islands of vegetation with a deeply eroded soil profile at Liawenee Moor.

Geology and Soils

A predominantly continuous sheet of Jurassic dolerite, several hundred meters thick, with some overlying outcrops of Tertiary basalt lavas and plugs, and localised Triassic sedimentary rocks underlie the Central Plateau (Banks 1973). The thick sheets of dolerite were injected from deep in the earth's crust c. 165 million years ago as molten rock. The horizontal sediments of the Parmeener Super Group beneath which the dolerite sheets cooled have been mostly removed by erosion except for small outcropping remnants. Tertiary basalt is prominent on Liawenee Moor, and few flows have been recorded between Great Lake and Lake Augusta – Lake Ada (Corbett 1996).

number of days when temperature drops below 0°C at Liawenee is 143 a year. Summers are cool, and winter minimum temperatures can fall below -10°C. Table 1.1 summarises several climate averages for Liawenee Station.

Figure 1.4 June snowfall around Liawenee hut.

Table 1.1 Climate averages for 096065 Liawenee Comparison. Latitude (deg S): -41.8997; Longitude (deg E): 146.6661. Commenced: 1984; Last record: 2004. Bureau of Meteorology 2004.

Element	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Annual	Number of years	Percentage complete
Mean daily Max Temp °C	18 6	18.7	16.2	12.6	9.2	6.2	5 5	6 4	9.1	12 1	14 7	17	12 3	15 4	87
Mean days where Max Temp ≥ 30 °C	0.3	0.3	0	0	0	0	0	0	0	0	0	0.1	0.6	15.4	87
Highest daily Max Temp °C	35	31.6	29.5	24	19 8	14.5	12.1	16.8	19.2	25.4	29 5	32	35	15.4	87
Mean daily Min Temp °C	5 5	5 5	3 7	2	0.3	-1.1	-1.5	-1 8	-0.5	0.7	2.1	3.9	1 6	15 4	87
Mean days where Min Temp ≤ 2 °C	6.1	5.9	10 9	16.2	22.7	24.7	27.3	28.1	23.7	21 9	15 7	11.1	214.3	15 4	87
Mean days where Min Temp ≤ 0 °C	2.1	1.8	4 4	9.4	16.3	19 2	21.3	23 6	17 9	14.3	9	4 7	143.8	15 4	87
Lowest daily Min Temp °C	-4	-3 5	-5	-6 5	-7.5	-10.4	-9 5	-8	-7 7	-6	-5 6	-4.3	-10.4	15.4	87
Mean 9am air temp °C	11.5	10 7	8.6	6 9	3 9	1 5	1 1	1 5	4	6	8.1	10.3	6 4	13.5	89
Mean 9am RH %	72	77	82	84	89	92	93	89	83	77	73	71	81	11.3	75
Mean 9am wind speed km/h	10 3	10 2	8 6	10 6	9.4	8 6	9.3	9.8	11.7	13 6	11 1	12.3	10 5	14.2	80
Mean 3pm air temp °C	17	17	14.8	10 8	7.5	4.7	4 1	5 2	7 3	10 6	12.9	15.3	10.8	13.5	89
Mean 3pm RH %	56	55	59	69	76	82	84	76	71	61	59	57	66	11.3	75
Mean 3pm wind speed km/h	14.9	14.3	13	13.1	11.1	10.7	11.4	13.3	13.5	17.1	15.2	14.8	13 6	13	79
Mean monthly rainfall mm	73.1	47.9	56 4	78 4	89.3	101.7	133.6	129 8	110.7	99.5	75	72 2	1067.6	18 6	94
Median monthly rainfall mm	66	39.4	42.4	67 4	73.8	92 7	133.6	127.8	91.6	86.6	70 8	60.2	1073.5	18	
Mean raindays	13.3	10.1	13 8	17.1	18.3	20.8	22.8	22 6	19 7	19	16.2	13.6	207 2	17.3	88
Highest monthly rainfall mm	230.2	138.6	137	172	203 8	174.6	210.4	244	241 2	211	137 6	160 8		18 6	94
Lowest monthly rainfall mm	16.4	2.8	10 6	17.8	21.2	53.2	57 6	40 6	54 8	53.8	23 4	18.8		18.6	94
Highest recorded daily rainfall mm	44.2	48	84.4	98	69.8	50.8	71 2	52	43	32	50	68 4	98	18.3	93
Mean clear days	6.1	5.7	5.3	3.9	3.8	3 7	3	3 7	2 5	2.8	4	5.1	49.4	13 8	90
Mean cloudy days	10 1	8 2	9 6	11.1	12.1	13.1	15.2	12.9	12.5	11.6	10.3	9 5	136.2	13.8	90
Mean daily hrs sunshine	8.7	8.6	7 6	5.7	4.7	3.6	3.6	5.2	6	7 7	8 4	8.9	6.6	10.6	93
Mean daily evaporation mm	4	3.7	2.5	1.4					1.3	2.5	3.2	3.9	3.1	6.7	55

Vegetation

The vegetation of the Central Plateau has been described by Jackson (1973) and Kirkpatrick (1983), and the section within the Tasmanian World Heritage Area has been comprehensively mapped at 1:25000 scale (Corbett 1996). McKenny (2000) mapped the vegetation of the Central Plateau Conservation Area east of Great Lake.

Glaciation, through its major effect on local topography and soil development is one of the major determinants of vegetation (Corbett 1996), with inverted, rather than altitudinal tree lines more common (Cullen 1995). The climatic treeline is reached at c. 1200-1300 m (Gibson & Kirkpatrick 1989), and even small variation in topography affects cold air drainage, soil drainage and exposure. Consequently, the vegetation on the plateau is a structurally and floristically diverse mosaic of plant communities. The vegetation ranges from forest and woodland, with canopies dominated by rainforest species, eucalypts, or *Athrotaxis cupressoides*, to treeless alpine communities, including shrubby heath and grassy heath, wet area sedgelands, *Sphagnum* bogs and herbfields (Corbett 1996). The Ada/Augusta grasslands form a unique succession (Corbett 1996).

There is limited information on the plant communities that existed before grazing so it's difficult to gauge how much the landscape has changed. According to Jackson (1973), prior to 1900 Liawenee Moor was covered by a tall tussock grassland of *Poa billardierii* and *P. gunnii* in the wetter parts, with a rich inter-tussock herb cover. Pollen studies from Camerons Lagoon at the southern end of Liawenee Moor also indicate a shift from grassland to grassy heath and the introduction of exotics with the first European settlement 175 years ago (Thomas & Hope 1994). Charcoal deposits in the core have been interpreted as evidence of the increased burning regime following stock introduction.

Fauna

The Central Plateau region provides a wide variety of habitat for animal species. Native vertebrate grazers commonly observed in the study areas included wombats, wallabies and pademelons. Rabbits were also sighted on a regular basis in the vicinity. Table 1.2 lists some other native and introduced fauna recorded in the surrounding area. Selected bird species occurring in the area are listed in Table 5.2.

Table 1.2 Mammal, amphibian and reptilian species recorded from the vicinity of the study sites (Natural Values Atlas database, Department of Primary Industries and Water 2006). Names in bold indicate introduced species.

Capra hircus	**goat**
Cervus dama	**fallow deer**
Felis catus	**cat**
Oryctolagus cuniculus subsp. cuniculus	**rabbit**
Sarcophilus harrisii	tasmanian devil
Dasyurus viverrinus	eastern quoll
Dasyurus maculatus subsp. maculatus	spotted-tailed quoll
Antechinus swainsonii subsp. swainsonii	dusky antechinus (tasmanian) or dusky antechinus
Thylogale billardierii	tasmanian pademelon or pademelon
Macropus rufogriseus subsp. rufogriseus	bennetts wallaby
Perameles gunnii	eastern barred bandicoot
Pseudocheirus peregrinus subsp. viverrinus	ringtail possum
Trichosurus vulpecula subsp. fuliginosus	brushtail possum
Bettongia gaimardi	tasmanian bettong or bettong
Vombatus ursinus subsp tasmaniensis	common wombat or wombat
Ornithorhynchus anatinus	platypus
Tachyglossus aculeatus subsp. setosus	echidna
Pseudomys higginsi	long-tailed mouse
Mus musculus	**house mouse**
Austrelaps superbus	copperhead snake
Niveoscincus ocellatus	ocellated skink or spotted skink
Niveoscincus metallicus	metallic skink
Litoria ewingi	brown tree frog
Crinia signifera	brown froglet

Study sites

Figure 1.5 shows the location of all study sites where the work was carried out and Table 1.3 summarises major site characteristics. All study sites lie below the climatic treeline, but are alpine as described by Kirkpatrick (1983). The communities focused on in this study were alpine heath, the most typical, but exceedingly variable, vegetation of Tasmanian alpine country (Kirkpatrick 1983; Kirkpatrick & Bridle 1999).

None of the sites have been burnt for at least 30 years (Bridle 1987). All the study sites are dominated by either *Grevillea australis* or *Orites acicularis*, or both. Both shrub species are known to be obligate seed regenerators (Williams & Ashton 1988; Kirkpatrick *et al.* 2002), which do not survive fire (Wahren *et al.* 2001). The presence of *Orites acicularis* has therefore been interpreted as indicating a climax community (Kirkpatrick 1983). This successional stage would be consistent with the 30-50 year cycle of shrub establishment, growth and senescence in these highly dynamic alpine communities suggested by Williams and Ashton (1988). *Ozothamnus hookeri* on the other hand, also present at Liawenee Moor and the western lakes study sites, is considered an early successional shrub, resprouting after fire and rapidly reaching reproductive maturity (Kirkpatrick *et al.* 2002). *Orites revoluta* can also recover vegetatively (Kirkpatrick *et al.* 2002).

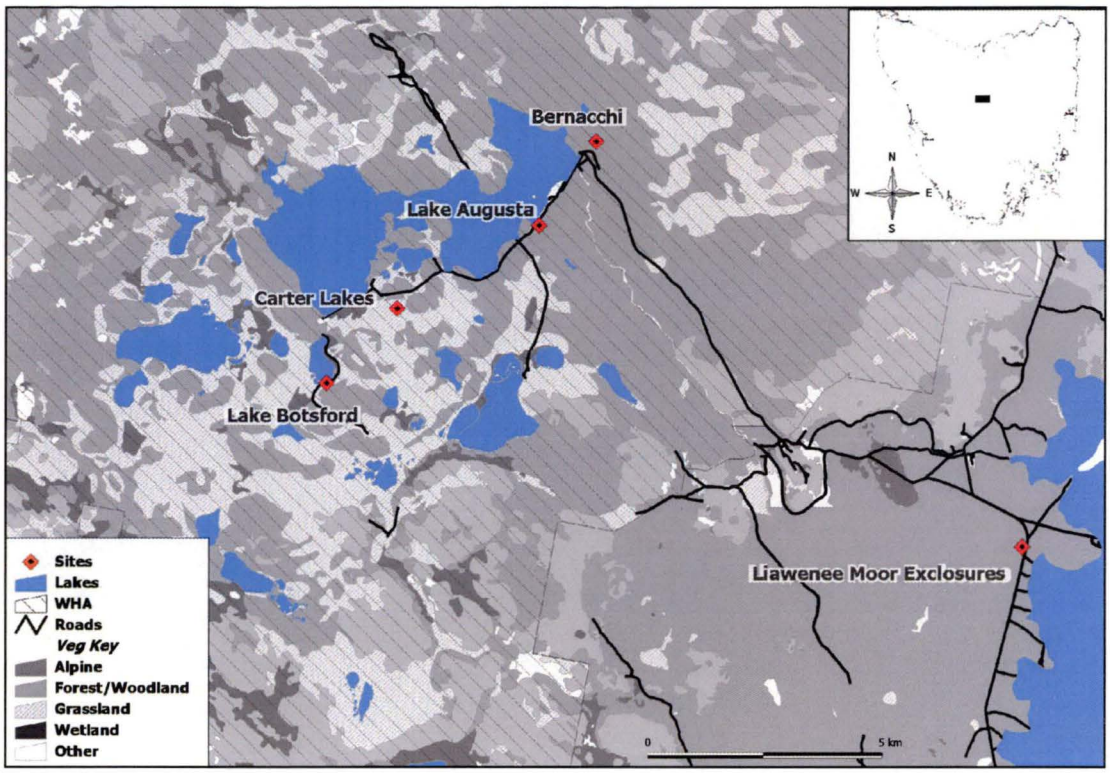


Figure 1.5 The location of study sites on the Central Plateau.

Grevillea australis was common to all study sites. The shrub has very variable habit and leaf form, especially in Tasmania (Figure 1.6). It ranges from a prostrate, spreading ground cover to an erect shrub up to 2 m tall, with both habits often co-existing at the one location.

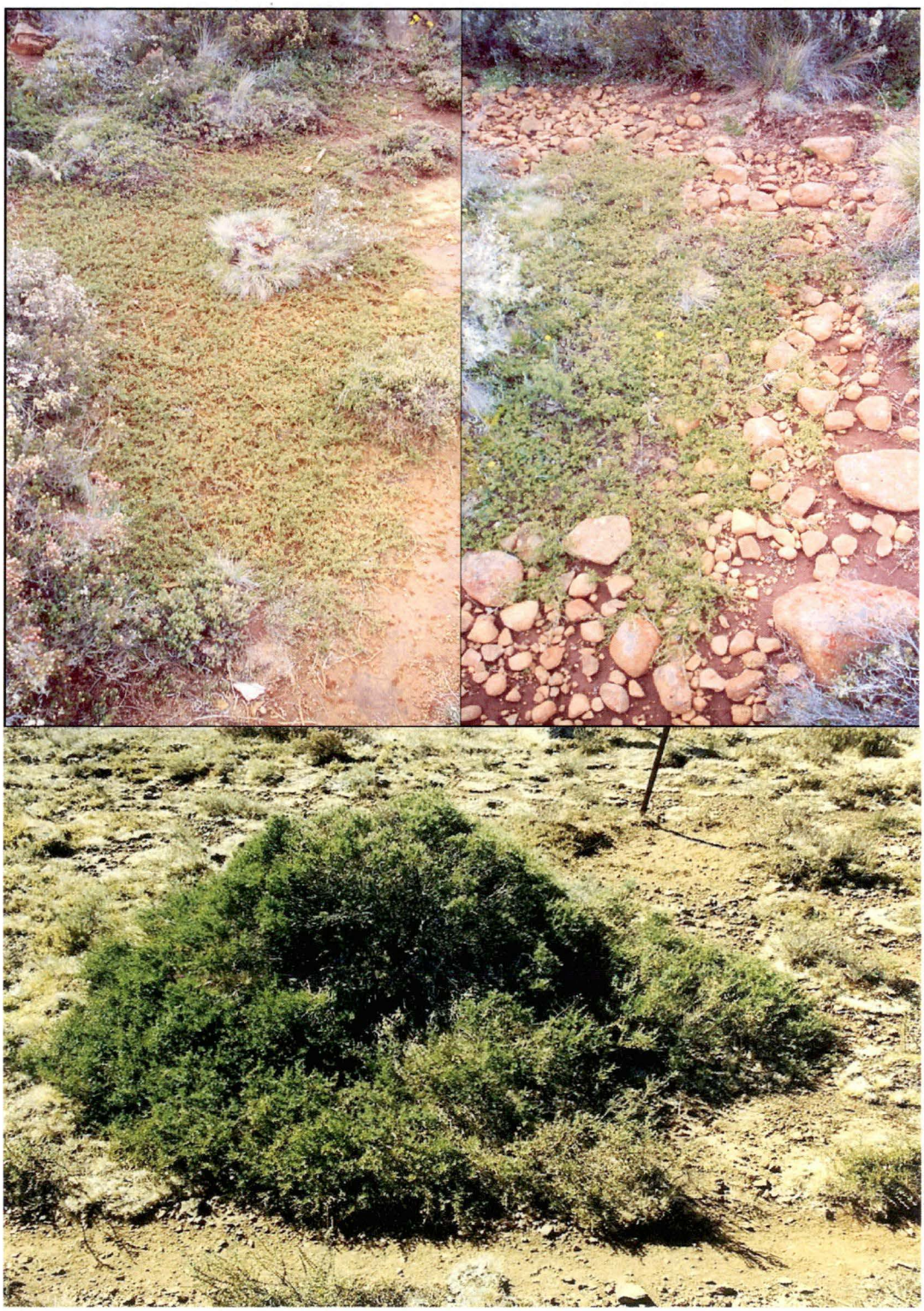


Figure 1.6 Prostrate form of *Grevillea australis* covering eroded gaps at Lake Botsford (above), and erect *Grevillea australis* shrubs outside grazing exclosures at Liawenee Moor (below).

Table 1.3 Summary of site characteristics.

Site	Elevation (m a.s.l.)	Geology	Vegetation type	Dominant species	Other common species/families	Fire and grazing history
Liawenee Moor Exclosures 41°55'06"S, 146°41'09"E	1050	basalt	alpine grassy shrubland	*Grevillea australis* *Poa* spp	Epacridaceae Asteraceae Poaceae *Coprosma moorei*	Patchily burnt by graziers until 1978. No stock grazing in Exclosures since early 1960s
Bernacchi 41°50'22"S, 146°34'51"E	1160	dolerite	shrubby alpine heath	*Orites acicularis* *Orites revoluta*	Epacridaceae *Grevillea australis* Poaceae	No fire since 1961, domestic stock grazing ceased in 1989
Lake Augusta 41°51'06"S, 146°34'01"E	1150	dolerite	shrubby alpine heath	*Orites acicularis* *Orites revoluta*	Epacridaceae *Grevillea australis*	Ada/Augusta grasslands patchily burnt until 1978, stock ceased grazing in this area c 1980.
Carter Lakes 41°52'15"S, 146°31'14"E	1140	dolerite	shrubby alpine heath	*Orites acicularis* *Orites revoluta*	Epacridaceae *Grevillea australis* Asteraceae	
Lake Botsford 41°53'22"S, 146°30'27"E	1150	dolerite	shrubby alpine heath	*Orites acicularis* - *Grevillea australis*	Epacridaceae Asteraceae *Orites revoluta* Poaceae *Luzula* spp.	

Liawenee Moor Exclosures

Liawenee – fresh, cold water – is one of many Aboriginal names assigned to areas of the Plateau developed by the Hydro-Electric Commission or other activities (Stancombe 1973). As this is private land, sheep usually graze on the moor during late spring, summer and autumn (November to May), and Liawenee Moor was patchily burnt by graziers until 1978 (Bridle & Kirkpatrick 1999). However, two 100 × 30 m exclosures (native herbivore and rabbit grazed plus no grazing, with sheep excluded from both) were established by the Department of Agriculture in the late 1960s, approximately 7 m from the road (Bridle & Kirkpatrick 1999). All work at the Liawenee site for the present study (except some seed collecting) was carried out within these plots (Figure 1.7)

Figure 1.7 Liawenee Moor site, a) view east in ungrazed exclosure, b) view west outside ungrazed exclosure

Both exclosures had greater vegetation cover, and greater frequency of many grasses and tall herbs than the surrounding vegetation exposed to grazing pressures (Bridle & Kirkpatrick 1999). Both forms of *Grevillea* occurred in the exclosures, but only the

erect habit was found outside the fenceline, where trampling by sheep prevented growth of the prostrate form. Although some Grevilleas within the herbivore-free exclosure were at the senescent stage and appeared to be replaced by a grass and herb understorey, small, and therefore young, *Grevillea* plants were in plentiful supply, ensuring the area within the fenceline remains a shrubby grassland for a number of years (Figure 1.8). This progression from shrubby heath to grassland has also been observed in the absence of grazing in the alpine and subalpine areas of mainland Australia (Wimbush & Costin 1979; Williams & Ashton 1988; Wahren *et al.* 1994).

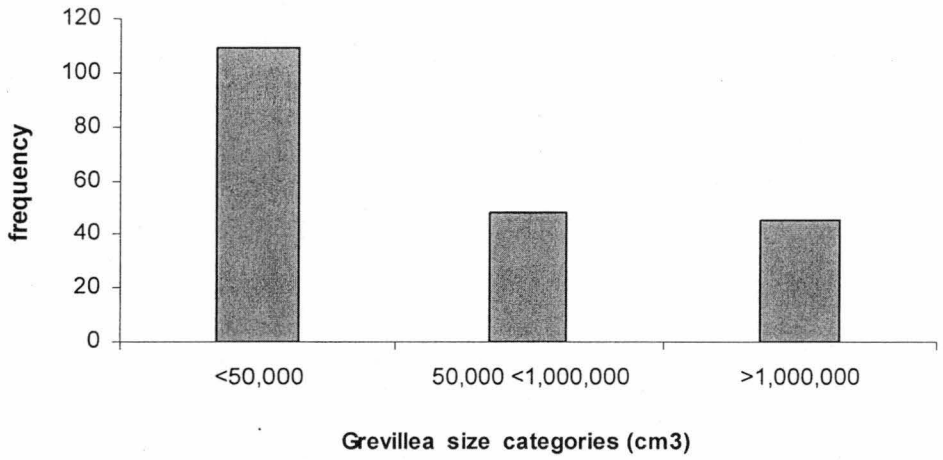


Figure 1.8 Population structure of *Grevillea australis* in herbivore-free exclosure at Liawenee Moor. N = 202, volume of shrub (cm^3) obtained by measuring height, width and length to the nearest cm.

Bernacchi

This alpine heath site is 1160 m a.s.l. and is dominated by a mosaic of Epacridaceae and Proteaceae, including, *Orites acicularis*, *O. revoluta*, *Grevillea australis, Richea acerosa, Epacris gunnii, Leucopogon montanus*, and *Pentachondra pumila. Ozothamnus hookeri*, as well as *Poa gunnii* are also common (Figure 1.9). No fire has occurred at this site since 1961 (Corbett 1996; Johnson & Marsden-Smedley 2001). The area is accessible to native and introduced herbivores, but domestic stock grazing ceased

in 1989, hence at this site, *Grevillea* was predominantly found as a prostrate ground cover.

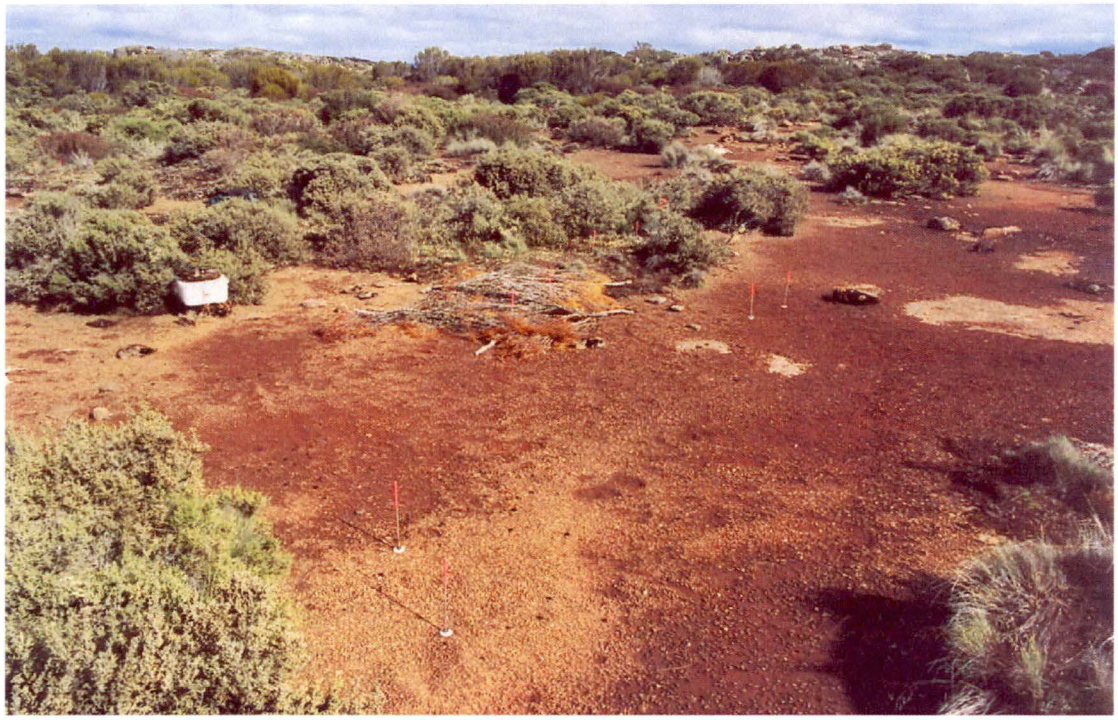


Figure 1.9 Scattered vegetation at the Bernacchi study site.

Carter Lakes, Lake Augusta and Lake Botsford

These shrubby alpine heath sites are situated at approximately 1140 - 1150m a.s.l., on the south-eastern and southern side of Lake Augusta. The sites are dominated by *Orites acicularis, O. revoluta, and Grevillea australis* (Figure 1.10 and Figure **1.11**). *Grevillea* occurred predominantly as a prostrate ground cover, but erect shrubs were also present. Proteaceae and Epacridaceae are the two major families found at this site. Common shrub species in the area include *Leucopogon montanus, Olearia algida, Ozothamnus hookeri, Richea acerosa,* and *Epacris gunnii. Pentachondra*

pumila, *Coprosma* sp, *Poa gunnii* and *Pterygopappus lawrenci*, as well as *Luzula*, *Brachyscome* and *Craspedia* spp. frequently occur in the lower strata. The Ada/Augusta grasslands were patchily burnt until 1978 (Corbett 1996), and stock ceased grazing in this area around 1980 (Bridle *et al.* 2001).

Figure 1.10 Carter Lakes site dominated by *Orites acicularis* shrubs.

Figure 1.11 Vegetation at Lake Botsford. Fenced exclosure is not a part of this study.

Chapter 2. Microclimate

INTRODUCTION

Seedlings growing in stressful environments such as arid, semiarid, alpine or arctic regions often benefit from some form of physical surface protection which enhance conditions for germination and establishment. Moss mats (Carlsson & Callaghan 1991), cryptogamic crusts, rocks, cushion plants (Pérez 1987; Anderson & Bliss 1998; Arroyo *et al.* 2003; Cavieres *et al.* 2006), shrubs (Brittingham & Walker 2000; Gomez-Aparicio *et al.* 2005; Henriquez & Lusk 2005), and neighbouring herbaceous vegetation (Ryser 1993) have all been reported to positively influence the establishment and survival of seedlings. Facilitation of establishment by existing vegetation is often attributed to the pioneer or nurse species exerting an ameliorating effect on the microclimate in its immediate vicinity, by buffering extreme temperatures and increasing moisture, stabilising the substrate, or reducing light intensity (Carlsson & Callaghan 1991; Ryser 1993; Brittingham & Walker 2000; Henriquez & Lusk 2005).

In alpine areas, short growing seasons, excessive radiation, desiccating winds, and low temperatures, coupled with ground disturbance by needle ice and soil frost heave, can severely limit plant colonization of open, unprotected areas (Gradwell 1960; Körner 1999). Without the insulating properties of plant cover, which prevents heat loss at night and shields the surface during the day, bare soil experiences greater daily oscillations in temperature relative to those under a vegetation canopy. In winter, vegetation acts as an insulator to reduce the rate of heat loss from the soil. Consequently frost penetration is more rapid and the depth of freezing is greater in bare soils than under a vegetative cover (Jury *et al.* 1991). Freezing temperatures, interacting with high irradiance, as occurs in open areas on cold winter mornings, can also cause photodamage to leaves and induce photoinhibition, thus reducing seedling growth and survival.

Shading by nurse plants, or adjacent vegetation, can ameliorate this low temperature stress (Egerton *et al.* 2000).

Although many studies have reported nurse effects in alpine or arid habitats, the microclimate amelioration behind this positive species interaction is often speculated rather than investigated quantitatively. If microclimatic parameters are recorded, they are often inadequate in terms of duration, or the frequency or number of measurements made. Importantly, there are no published microclimate studies which describe differences between bare and vegetated microhabitats in an Australian alpine system.

This study tested the hypothesis that there are detectable microclimate differences in bare and sheltered microhabitats, such as under *Grevillea* shrubs, jute matting or *Orites acicularis* slash. In particular, soil surface temperature was expected to have lower daily amplitude, lower daily maxima and higher daily minima in sheltered microhabitats, while surface relative humidity was expected to be higher and wind speed and solar radiation was expected to be lower than in exposed microhabitats. Consequently, the frequency of freeze-thaw cycles and amount of soil frost heave was expected to be greater in open microhabitats also. Such differences would contribute to the inability of seedlings to colonize gaps in the vegetation and close them over time.

METHODS

Microclimate studies were carried out at Liawenee Moor Exclosures and Bernacchi. Frost heave measurements were taken at Liawenee Moor Exclosures, Carter Lakes, Lake Augusta, and Bernacchi. For site descriptions see Chapter 1.

Temperature and relative humidity

To measure microclimatic parameters under a *Grevillea* shrub and in an adjacent bare patch, a Grant 1000 Series (Type 1023) Squirrel Meter/Logger (Squirrel 1) was installed at Liawenee Moor in the all herbivore exclosure on 23 November 2000 (Figure 2.1). Eight type K (Chromel-Alumel) thermocouple channels (-200 to 200°C, resolution 0.1°C) logged soil surface temperature, with four thermocouples placed randomly under *Grevillea* and four in the bare patch. In addition, two Rotronic HygroClip® (Rotronic AG, Zürich, Switzerland) temperature and humidity sensors (measuring range –40 to 85°C, 0-100% RH; accuracy ±0.3K, ±1.5%RH) were wired to voltage current channels (resolution 0.5mV) to obtain relative humidity and an additional soil surface temperature reading in the two microhabitats. In December 2000, a second logger (Squirrel 2) was set up in another *Grevillea* patch at the other end of the exclosure. Soil surface temperature was measured with type K thermocouples as above, but Vaisala humidity probes (type HMP35DGT, measuring range 0-100%, accuracy ±1%RH), which could not be wired for temperature readings on this Squirrel model, were used instead of the Rotronic sensors. All sensors were shielded with hemispherical PVC screens (Figure 2.1).

The loggers were powered by six AA manganese-alkaline batteries or an external 12V DC battery at 100 mA, which was housed with the loggers in a wooden or plastic box packed with bags of silica beads. The Squirrels were downloaded approximately once a month in the field using Eltek SQREM V3.21 software. The batteries were also changed or charged at this time, and any faulty or damaged thermocouples were replaced.

Figure 2.1 Microclimate logging system, with sensors (shielded) and a Squirrel Logger plus external battery (in boxes) at Liawenee Excolsures.

The Squirrels were programmed to sample data from all sensors every 60 seconds and log the average of these readings every 20 minutes. This programming time made optimal use of logger memory and battery life. The data was used to calculate daily minimum soil surface temperature, freeze-thaw events around –0.5/0.5, -2.0/0.5 and –5.0/0.5 thresholds, as well as the number of hours under the thresholds (see Sinclair 2001). These values were chosen because the 0°C threshold does not necessarily correspond with the freezing point of soil water due to the presence of solutes, and needle ice requires a soil surface temperature of at least -2°C (Outcalt 1971; Lawler 1988). Although the daily maximum temperature would have been of interest also, the quality of those readings was problematic. While the sensors were shielded from direct sunlight to avoid measuring the heating properties of the metal junction rather than the ambient conditions (Unwin 1980; Pearcy *et al.* 1989), it was nevertheless difficult to avoid sunlight heating the sensors early in the morning and late in the afternoon due to the low solar angle, often resulting in higher values at those times of the day than at

midday. The shields were also sometimes displaced or heaved out altogether during the winter months, rendering the maximum values unreliable. The same problem was encountered when the thermocouples were inserted below the soil surface to minimize potential radiation errors. Encasing the sensors in a larger structure on the other hand would have changed the ambient conditions too greatly for the purpose of this study.

Originally attempts were made to record soil temperature at depths of 5 and 10 cm also, but due to frost heave activity displacing the probes, and lack of replication in case of thermocouple failure this was abandoned during the first autumn of monitoring.

Solar radiation (PPFD)

Photosynthetic Photon Flux Density (PPFD) under *Grevillea* and on bare ground was recorded with two LiCor Li-190SB quantum sensors (Figure 2.2) which were wired to a LI-1000 data logger (Li-Cor Inc., Lincoln, Nebraska, USA) powered by an external 12 V DC battery at 100 mA. Maximum, minimum, and integrated Photosynthetically Active Radiation (PAR) values (as μmol m^{-2} s^{-1} and mol m^{-2}) were logged every 30 minutes (sampling interval 5 seconds). The logger and two sensors were placed in conjunction with Squirrel 1 and downloaded at the same time using HyperTerminal. The logger was first deployed on 11 July 2001 and removed on 17 April 2003.

Figure 2.2 LiCor Li-190SB Quantum sensors under *Grevillea australis* canopy, and in an adjacent gap.

Wind speed

Wind speed was measured periodically with two thermoanemometers (platinum sensor, measuring range 0-2V), one in *Grevillea* and one in an adjacent bare area (Figure 2.3), which were connected to two voltage current channels on Squirrel 2 and to an external 12 V battery (at 100mA). The sensors were positioned to face the direction of prevailing wind, either west or southwest, depending on the conditions on the day. The wind speed measurements were sporadic due to the high power consumption of the sensors and the requirement for dry weather when using them. The sensors were calibrated using a cup anemometer. Thermoanemometers were a better choice in this study than cup anemometers as they can measure very low velocities, could be placed only 10cm from the soil surface in the dense *Grevillea* shrub, and did not have problems with overrunning or maintenance of moving parts. Data was collected on 16 days, between April 2002 and 2003.

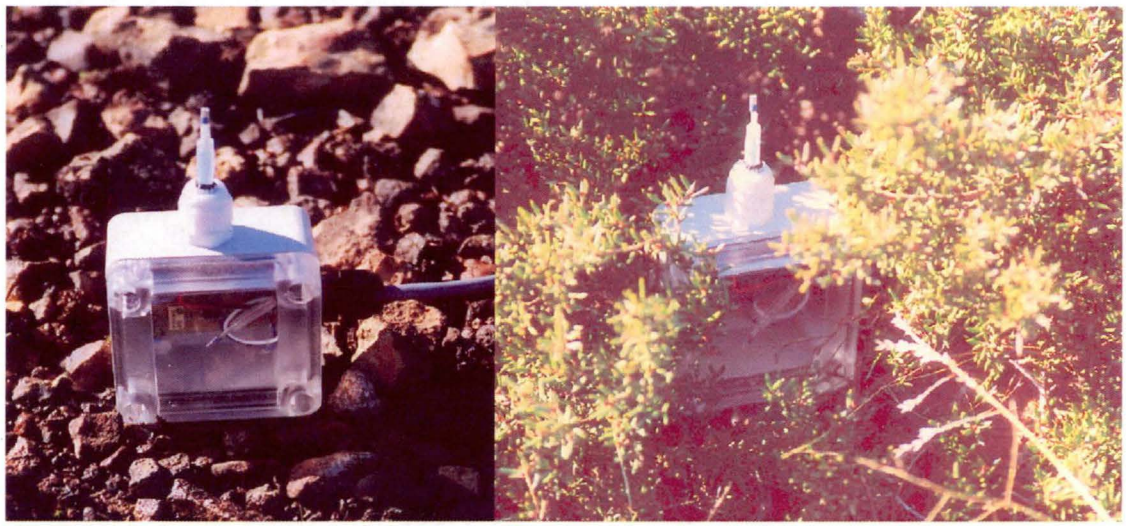


Figure 2.3 Thermoanemometers in gaps, on left, and amongst *Grevillea australis* branches, on right.

Data homogeneity

Squirrel 1 collected data continuously from 23 November 2000 until 25 June 2001. At that point, the Squirrel was removed due to damage from flooding, possibly from accumulated snowmelt. A replacement Squirrel 1 was set up six months later, on 28 December 2001, and was operational until 20 March 2003. Squirrel 2 logged continuously from 29 December 2000 until 19 April 2003. Some inhomogeneity of data was encountered with both Squirrels and Li-1000. This is difficult to eliminate completely in situations where data collecting in remote locations is automated. Breaks in data collection occurred due to miscellaneous breakdowns and malfunctions. The main problem encountered was failure of the thermocouples, usually due to mechanical damage at the wire junction which led to spurious reading caused by electrolytic effects or resulted in no readings being logged. Under low temperature conditions, internal battery life was limited and unpredictable, leading to gaps in data in between downloading trips. This was rectified by connecting an external 12 V battery as a back

up after the problem first occurred. Similarly, power failure also interfered with continuous Li-1000 data collecting.

Frost heave

Vertical Displacement Gauges (VDGs), based on a design used in the Circumpolar Active Layer Monitoring Programme (Brown *et al.* 2000), were used to measure the extent of diurnal soil frost heave (Figure 2.4). A gauge consisted of 5 mm diameter stainless steel pin, sharpened at one end, a rubber stopper and a wooden disc. The length of the pin varied between 30 to 50 cm, depending on the depth of soil at a given site. The pin was hammered into the soil to a depth of at least 10 cm, with the loosely fitting round piece of thin plywood and the more tightly fitting rubber stopper on top of it pushed down to ground level. The distance between the top of the pin and the top of the rubber stopper was recorded. As the soil heaved, it pushed the wood/rubber assembly up the pin. When the soil thawed, the wooden disc was lowered to the ground surface, but the rubber stopper remained at its displaced position on the pin. The distance between the tip of the pin and the top of the rubber stopper was recorded again after this movement occurred, giving a quantitative assessment of the frost heave. The VDGs were then reset by pushing the rubber stopper to ground level again, and another baseline measurement was taken.

Six VDGs were installed in bare patches, and two under *Grevillea* shrubs at Liawenee Moor Exclosures on 25 June 2001. Due to their successful operation, 12 more were added on 13 September 2001 to bring the total number in each microhabitat to 10, and another 10 were installed at Lake Augusta, five under *Grevillea* and five in open ground. Similarly, 10 VDGs were established at Carter Lakes on 26 October 2001. At the end of July 2002 five more VDGs were set up in each microhabitat at Lake Augusta. Likewise, in March 2003, six more VDGs were added at Carter Lakes, increasing the total to eight under *Grevillea* and eight in open ground. Monitoring concluded on 20 April 2003. Measurements were recorded daily where possible (for up to six consecutive days) approximately once a month. The first measurement of each monthly instalment was

indicative of the maximum frost heave event since the VDGs were reset after the previous set of measurements. No readings were recorded unless there was visible movement of the rubber stopper. At the unfenced sites (Lake Augusta and Carter Lakes), wombats (presumably) interfered with some VDGs, reducing the number of replicates. The bent pins were replaced with new ones in a different location. Snow cover also prevented measurements on a number of occasions in winter.

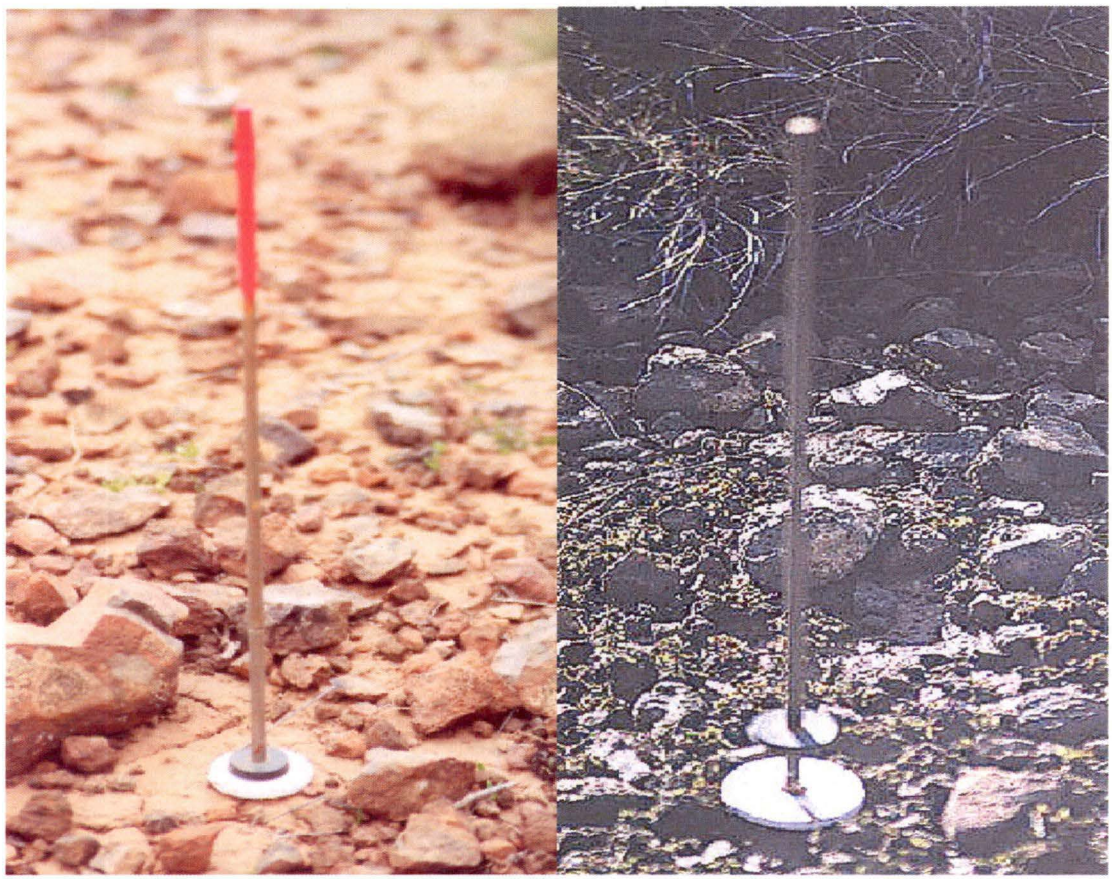


Figure 2.4 Vertical Displacement Gauges (VDGs). The image on the right shows the height of frost heave recorded by movement of the upper disc.

Bernacchi

In addition to comparing microclimate parameters under *Grevillea* shrubs and in bare patches at Liawenee Moor Exclosures, a site was set up to evaluate soil surface temperature, relative humidity and frost heave under jute matting and *Orites acicularis* slash, as well as in bare patches and under intact vegetation. Both jute matting and slash have been used previously in geoconservation work on the Central Plateau (Comfort 1999, 2000). A double jute mat 1 m wide x 2 m long and another replicate a few meters away were laid out in an eroded bare area adjacent to a patch of vegetation. Two squares of freshly cut *O. acicularis* branches approximately 1m x 1 m were set up in a similar way (Figure 2.5). All jute, slash, vegetation and bare replicates were within an area of approximately 6 m radius. An Eltek Squirrel 32 meter/logger recorded relative humidity with two Vaisala probes (HMP 31 UT, measuring range 0-100%, accuracy ±1%RH) from 6 March 2002 until 19 February 2003. Because only two channels were available for relative humidity sensors, the Vaisala probes were randomly rotated between the jute, slash, bare and vegetation patches. To monitor soil surface temperature in the four treatments, an Eltek Squirrel 80 meter/logger (16 type K thermocouple channels) was set up from 21 February 2002 to 18 February 2003, with four replicate sensors per treatment. Average readings were logged every 20 minutes on both Squirrels. The data was used to calculate daily minimum soil surface temperature, freeze-thaw events around –0.5/0.5, and –5.0/0.5 thresholds, as well as the number of hours under the thresholds for each microhabitat. The data was downloaded in the field approximately once a month with Grantware Filewise 1000 software, and any faulty thermocouples or flat batteries were also replaced at this time. Because this site was unfenced, there were recurring problems with animals chewing through the thermocouple wires, resulting in incomplete data sets for the study period.

In addition, between four and six VDGs were set up in each of the four microhabitats. The soil at the Bernacchi site was quite shallow, so anchoring the VDGs to a suitable depth of at least 10 cm was difficult. Consequently, many of the pins were easily heaved out, reducing the number of replicates.

Figure 2.5 Bernacchi site showing jute and *Orites* slash treatments with VDGs and Squirrel data logger (white box).

Data analysis

Relative humidity, solar radiation and wind speed could not be evaluated statistically due to the lack of replicate sensors for these parameters in the two microhabitats.

Soil surface temperature and freeze thaw

The daily minimum soil surface temperature data was analysed with a single factor ANOVA using general linear model (GLM) procedures in SAS ver.9.1 (SAS Institute Inc. 2002) with microhabitat type as the single fixed factor. Data from Liawenee Exclosures was analysed separately for Squirrel 1 and Squirrel 2.

A single factor ANOVA was performed on the number of freeze-thaw events around each threshold per month, and the number of hours spent below each threshold per month, with microhabitat (*Grevillea* canopy vs Bare) as the single fixed factor. Data from Liawenee Exclosures was analysed separately for Squirrel 1 and Squirrel 2.

Frost heave

A repeated measures single factor ANOVA using GLM procedures was performed on VDG displacement data for each measurement date, with microhabitat type as the single fixed factor (bare and *Grevillea* canopy at Liawenee Exclosures, Carter Lakes and Lake Augusta; and bare, intact vegetation, jute and *Orites acicularis* slash at Bernacchi). Sites were analysed separately due to different observation dates. Differences between measurements were compared *post hoc* using the Ryan-Einot-Gabriel-Welsch Multiple Range Test (Day & Quinn 1989).

RESULTS

Precipitation

Precipitation data was not collected in this study, however it does inform many aspects of microclimate and seedling dynamics, as well as seed production and the wider ecological processes relevant to regeneration. Therefore, Bureau of Meteorology precipitation data from Liawenee is presented for the study period (Figure 2.6 and Figure 2.7).

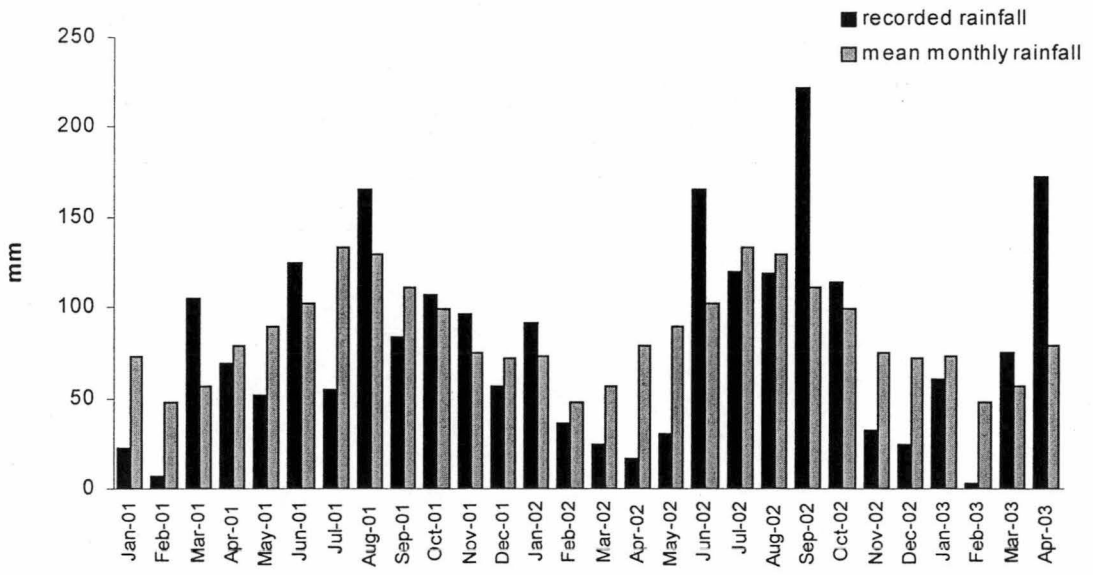


Figure 2.6 Total monthly precipitation (mm) recorded during the study period, and mean monthly precipitation for Liawenee climatological station. Data curtesy of the Bureau of Meteorology, Hobart.

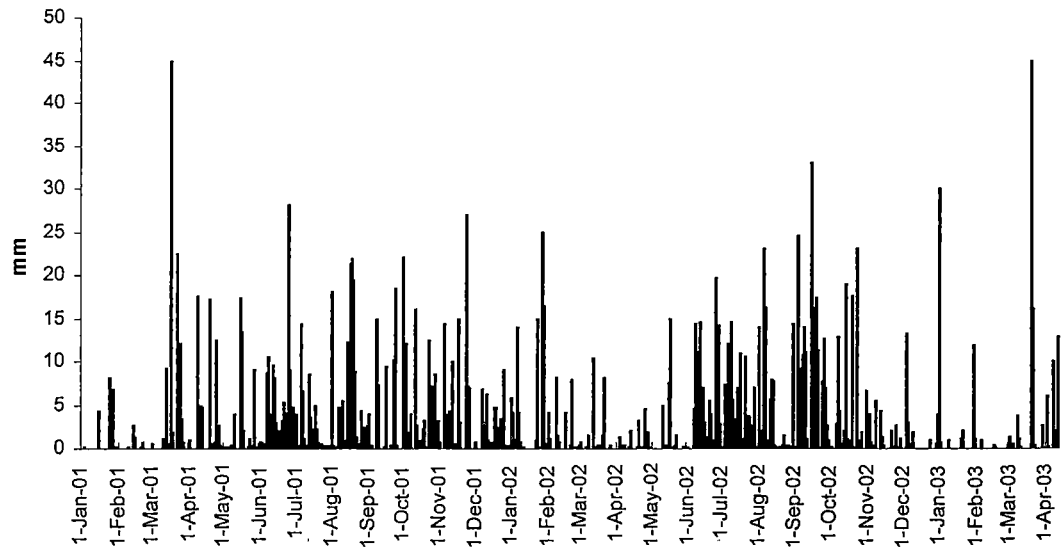


Figure 2.7 Daily total precipitation profile for the study period for Liawenee climatological station. Data curtesy of the Bureau of Meteorology, Hobart.

Relative humidity

Relative humidity in both microhabitats fluctuated seasonally and daily, with minimum values generally highest in winter and lowest in summer (Figure 2.8 and Figure 2.9). Daily minima close to 100% were common from May to November 2002, but during summer the amplitude of diurnal oscillations was greater. Daily minimum relative humidity between December 2002 and April 2003 was generally lower than for the same period in 2001/2002 (Figure 2.9). Daily maximum values were high throughout the year, predominantly over 80% RH. The lowest maximum readings recorded under the two Grevilleas were 62.1% and 68.4% on 25 January 2003, while bare ground reached 62.2% and 61.9%, also on the same day. Daily minimum RH values under *Grevillea* ranged from 12.3% and 15.7% (25 February 2003), and in open patches from 11.2% (also on 25 February 2003) and 12.7% (3 May 2003) to 100% during the night or on rainy days (Figure 2.8 and Figure 2.9).

While one location recorded generally lower daily minimum, maximum and mean values in the bare patch than under *Grevillea* throughout the time series (Figure 2.8), no such pattern was evident in data obtained from the other *Grevillea* and bare patch studied (Figure 2.9). Average relative humidity oscillations calculated from Squirrel 1 were also greater in the open than under *Grevillea* throughout the year, with differences of 70% between daily minimum and maximum readings common in bare patches during summer, but very rarely reaching those levels under *Grevillea*. The general pattern of relative humidity recorded reflected that of the Automatic Weather Station operated by the Bureau of Meteorology at Liawenee, approximately 2 km NW of the exclosures (Figure 2.10).

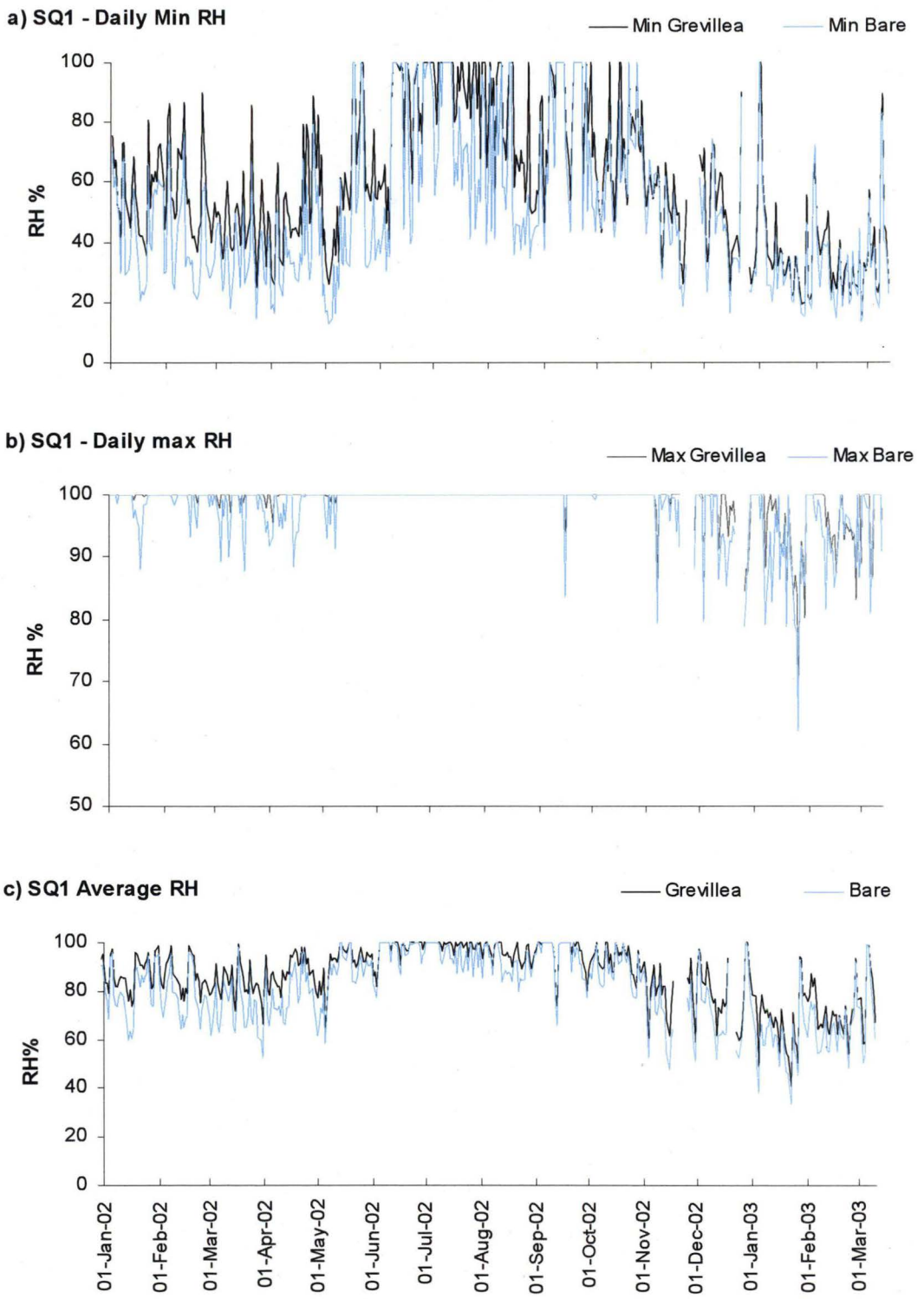


Figure 2.8 Daily minimum (a), maximum (b) and mean (c) relative humidity under *Grevillea* shrubs and in adjacent bare patches at Liawenee Exclosures. Data from Rotronic sensors connected to Squirrel 1.

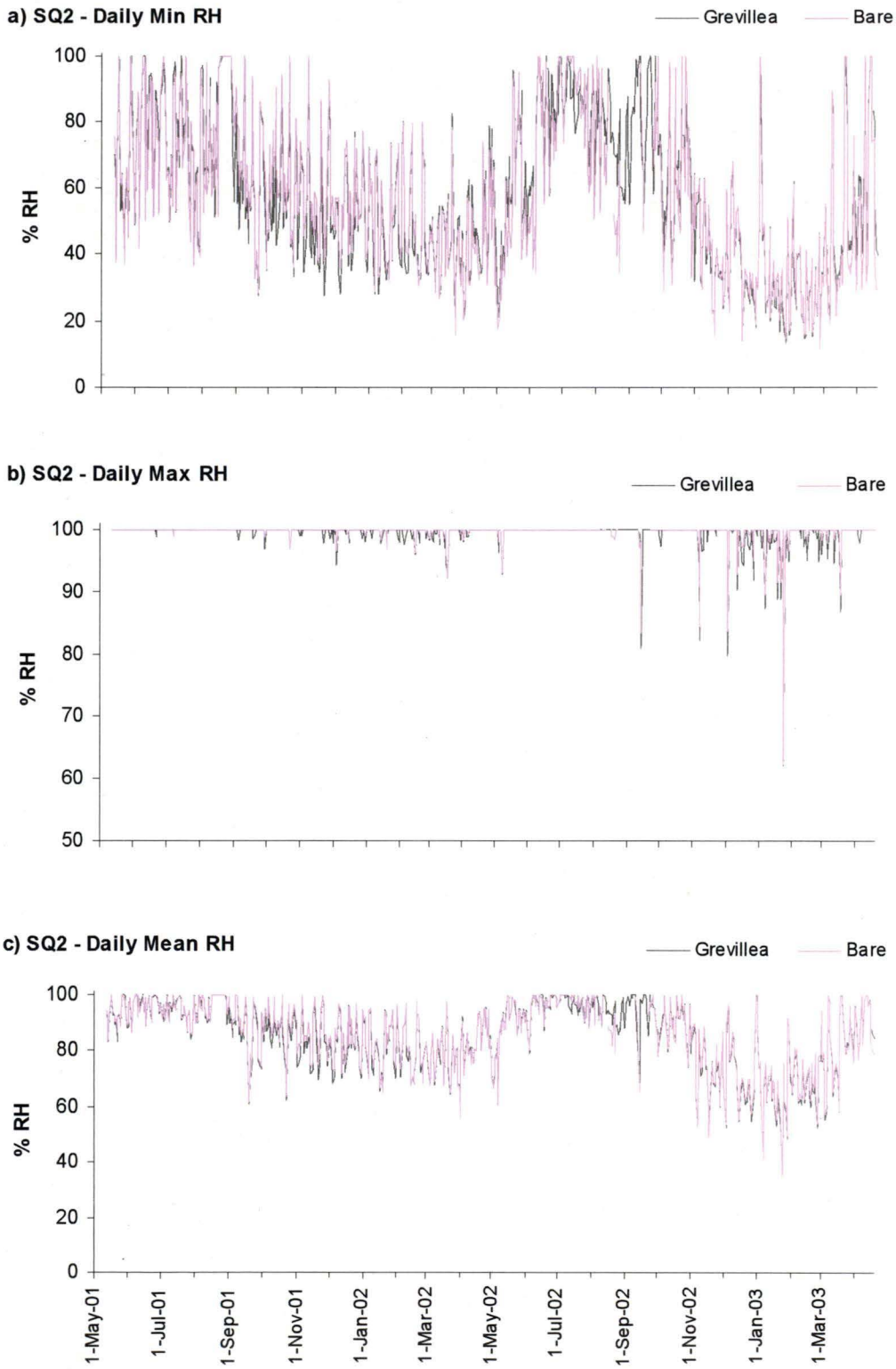


Figure 2.9 Daily minimum (a), maximum (b) and mean (c) relative humidity under *Grevillea* shrubs and in adjacent bare patches at Liawenee Exclosures. Data from Vaisala sensors connected to Squirrel 2.

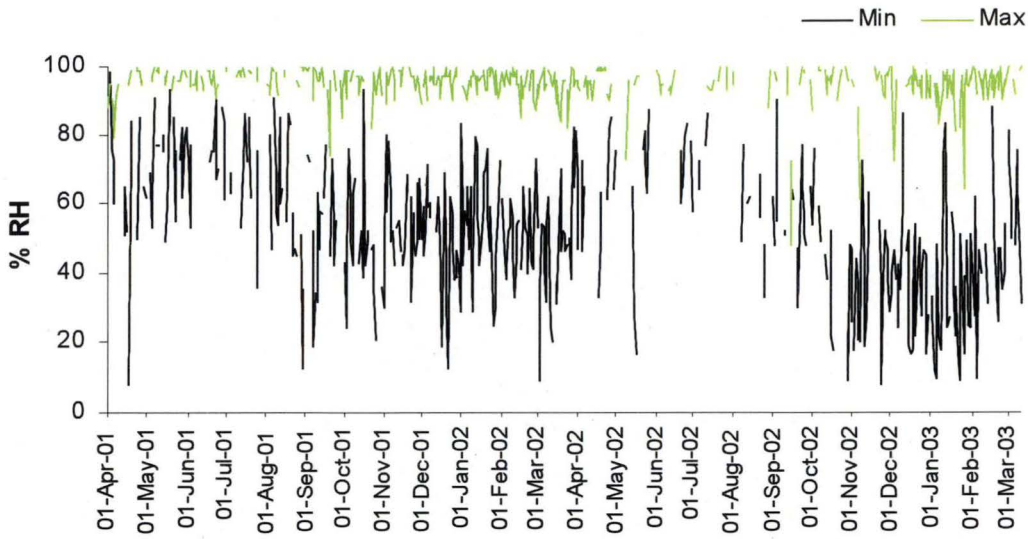


Figure 2.10 Daily minimum and maximum relative humidity based on hourly Liawenee AWS observations.

Soil surface temperature

Daily minimum soil surface temperature did not differ significantly between bare patches and *Grevillea* shrubs ($F_{1,2919}$=2.38, P=0.12, Figure 2.11 and $F_{1,3688}$=3.63, P=0.06 Figure 2.12). The range of temperatures recorded reflected those registered by the nearby Liawenee AWS (Figure 2.13). From May to November, minimum temperatures were predominantly below 0°C, but the lowest temperature recorded, -11.7°C, occurred on 21 April 2001 in a bare patch. Even during the summer months minimum temperatures remained mostly below 10°C, with the highest daily minimum of 13.6°C recorded on 18 March 2003 under *Grevillea*.

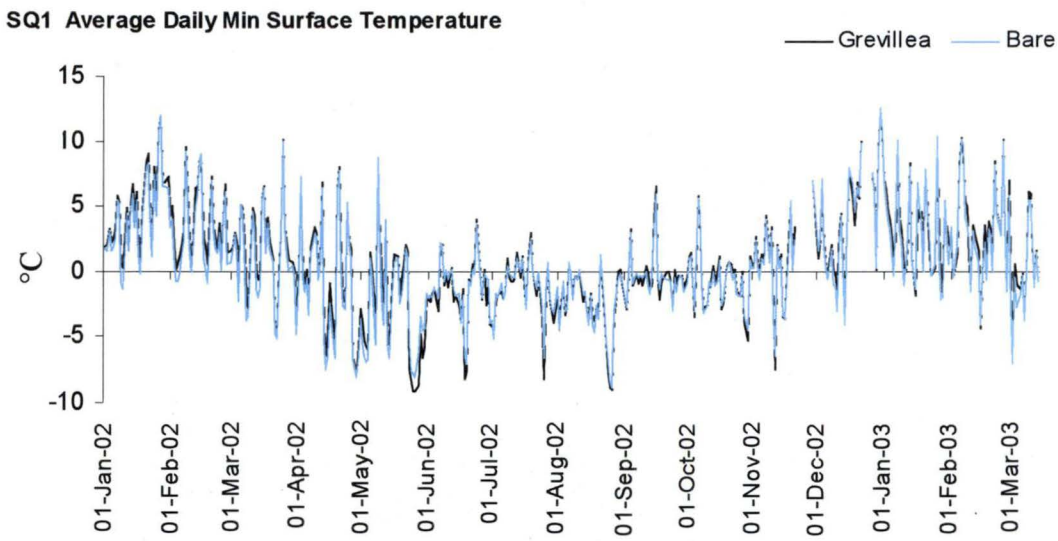


Figure 2.11 Daily minimum soil surface temperatures under *Grevillea* shrubs and in adjacent bare patches. The values are a mean of 3 to 5 thermocouples logged by Squirrel 1.

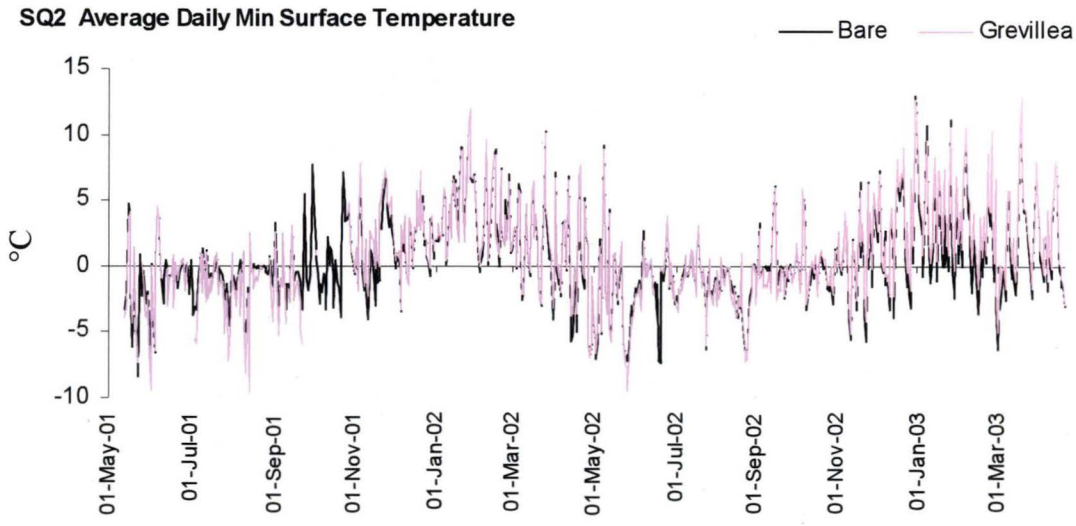


Figure 2.12 Daily minimum soil surface temperatures under *Grevillea* shrubs and in adjacent bare patches. The values are a mean of 2 to 4 thermocouples logged by Squirrel 2.

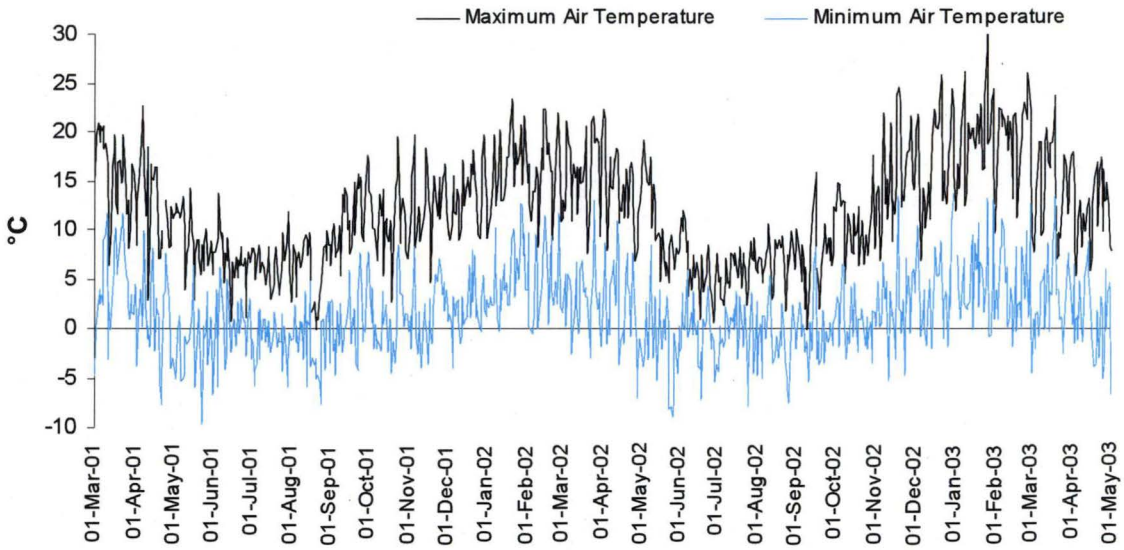


Figure 2.13 Daily minimum and maximum air temperatures from Liawenee AWS observations.

Freeze-thaw cycles

The frequency of above ground freeze-thaw events varied seasonally. Although more severe freeze-thaw cycles (below the -5.0°C threshold) were largely restricted to late autumn and winter, mild freeze-thaw events (above the –5.0°C threshold) did occur during the summer months (Figure 2.14). February 2002 soil surface temperatures did not fall below –2.0°C, with Squirrel 1 recording only one 1.3 hr event in bare ground in January 2002 (Figure 2.14). August 2002 had the highest mean number of all freeze-thaw events for both *Grevillea* (27.7 ±2.9 for SQ1 and 24.7 ±1.9 for SQ2), and bare microhabitats (24.8 ±2.9 and 23.5±2.5 for SQ1 and SQ2 respectively), which was more than twice the number of cycles recorded in August 2001 by SQ2. However, when the milder events are excluded, May 2002 had the highest number of cycles around the –5.0/0.5°C threshold (8 and 8.5 ±4.5 under *Grevillea*, and 10 ±1 and 8 ±1 in Bare, SQ 1 and SQ 2 respectively). More freeze-thaw events were also recorded in the 2002/2003 summer and early autumn (December – March) than in the same 2001/2002 period (Figure 2.14).

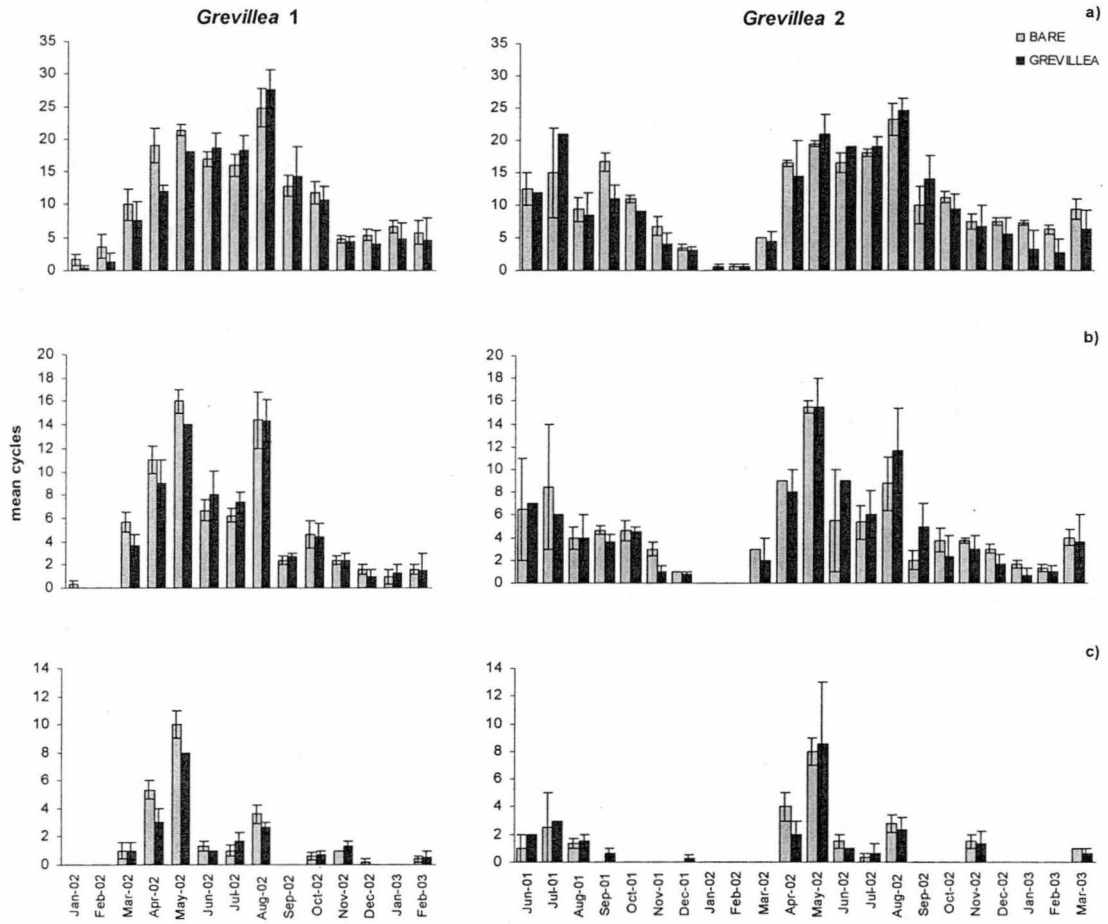


Figure 2.15 Mean monthly soil surface freeze–thaw events across a) -0.5/0.5, b) -2.0/0.5 and c) -5.0/0.5 °C thresholds under *Grevillea* shrubs and in adjacent bare ground. The values are a mean of 3 to 5 thermocouples (depending on month) logged by Squirrel 1 for *Grevillea* 1, and a mean of 2 to 4 thermocouples logged by Squirrel 2 at *Grevillea* 2.

There was no significant difference in the frequency of freeze-thaw events between *Grevillea* and Bare for any month for the total period of monitoring by either Squirrel, with a large degree of variability between thermocouples (Table 2.1 and Table 2.2). This was also the case for the mean monthly number of hours frozen below the given thresholds (Figure 2.16), which positively correlated with the mean monthly number of freeze-thaw cycles, reflecting a pattern of numerous diurnal oscillations around the set thresholds rather than extended periods between the thresholds. The only exception

occurred in September 2001 in *Grevillea* 2. In that month, bare ground remained significantly longer below the –0.5/0.5 °C thresholds than soil surface under *Grevillea* canopy ($F_{1,4}$=13.154, P=0.02).

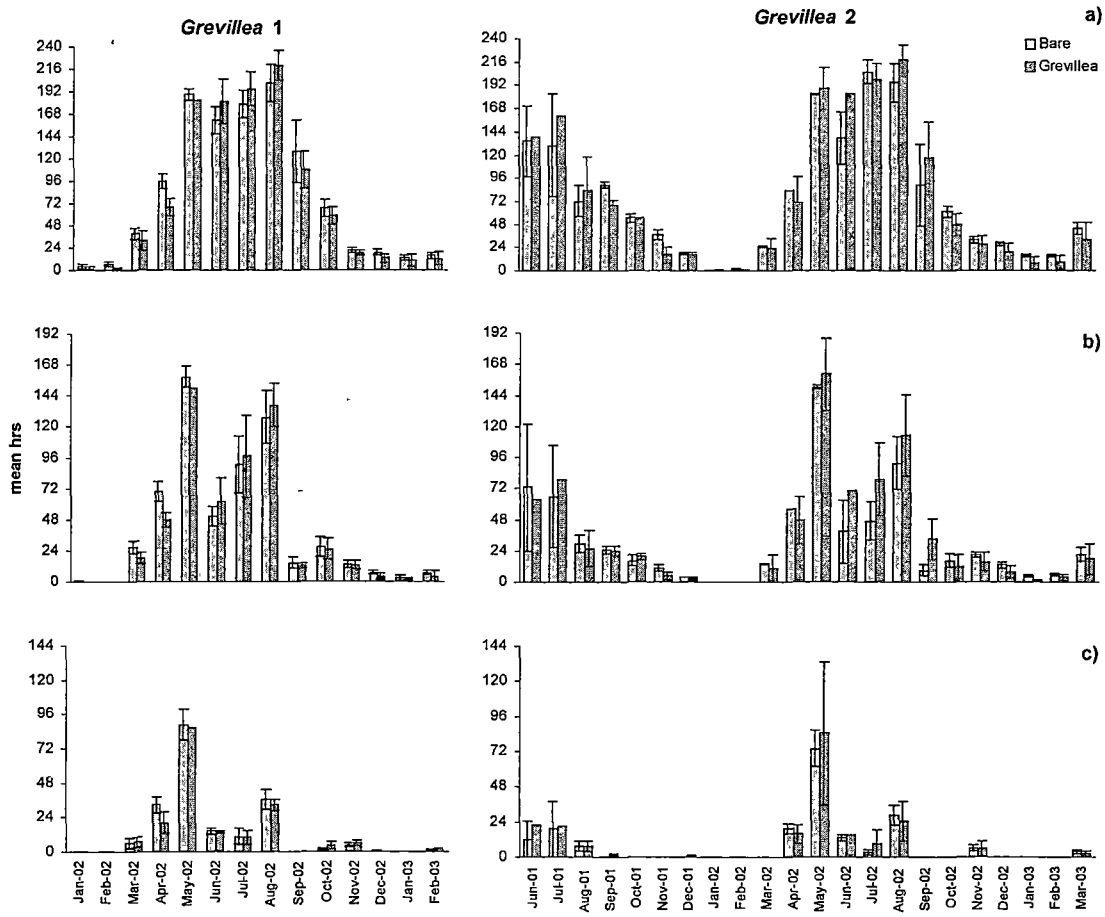


Figure 2.16 Mean monthly hours spent below the a) –0.5/0.5, b) – 2.0/0.5, and c) –5.0/0.5 °C thresholds under *Grevillea* shrubs and adjacent bare ground. The values are a mean of 3 to 5 thermocouples logged by Squirrel 1 at *Grevillea* 1, and a mean of 2 to 4 thermocouples logged by Squirrel 2 at *Grevillea* 2.

Table 2.1 Summary of ANOVA for effect of microhabitat on number of freeze thaw cycles a), and hours spent below each threshold b), in a given month for *Grevillea* 1. May 2002 not analysed due to lack of sensor replication, _ indicates 0 cycles, or 0 hours spent below threshold.

a)

	-0.5/0.5°C Cycles			*-2.0/0.5°C Cycles*			*-5.0/0.5°C Cycles*		
	F	df	P	F	df	P	F	df	P
Jan-02	2	1,4	0.230	1	1,4	0 374	_	_	_
Feb-02	1.114	1,4	0.351	_	_	_	_	_	_
Mar-02	0.426	1,4	0.550	2 571	1,4	0 184	0.000	1,4	1
Apr-02	4 009	1,3	0.139	0 900	1,3	0.413	4.200	1,3	0.133
Jun-02	0 455	1,4	0 537	0.348	1,4	0 587	1.000	1,4	0.374
Jul-02	0 722	1,5	0.434	1.068	1,5	0 349	0 816	1,5	0 408
Aug-02	0 414	1,6	0 544	0 000	1,6	0 985	0.993	1,6	0 357
Sep-02	0.154	1,6	0.708	0.207	1,6	0.665	_	_	_
Oct-02	0 169	1,6	0 695	0.021	1,6	0.889	0.027	1,6	0.875
Nov-02	0.214	1,6	0.660	0.009	1,6	0 929	1 429	1,5	0.286
Dec-02	0 563	1,6	0.482	0 779	1,6	0 411	_	_	_
Jan-03	0.727	1,6	0 427	0.117	1,6	0 744	_	_	_
Feb-03	0.129	1,5	0 734	0.009	1,5	0 927	0.042	1,5	0.846

b)

	-0.5/0.5°C Hours			*-2.0/0.5°C Hours*			*-5.0/0.5°C Hours*		
	F	df	P	F	df	P	F	df	P
Jan-02	0 679	1,4	0.456	1	1,4	0.374	_	_	_
Feb-02	3.197	1,4	0.148	_	_	_	_	_	_
Mar-02	0.416	1,4	0.554	1.479	1,4	0 291	0.031	1,4	0 869
Apr-02	5.238	1,3	0.106	3 891	1,3	0 143	1 896	1,3	0.262
Jun-02	0 484	1,4	0.525	0 398	1,4	0 563	0.151	1,4	0.717
Jul-02	0 493	1,5	0.514	0.032	1,5	0.864	0.003	1,5	0.960
Aug-02	0.421	1,6	0.541	0.101	1,6	0.761	0.178	1,6	0.688
Sep-02	0 187	1,6	0.680	0.159	1,6	0.704	_	_	_
Oct-02	0.326	1,6	0.589	0 016	1,6	0.903	1 145	1,6	0 326
Nov-02	0.467	1,6	0.520	0 034	1,6	0 860	0 419	1,5	0.541
Dec-02	1.209	1,6	0.314	0.968	1,6	0 363	_	_	_
Jan-03	0 287	1,6	0.611	0.274	1,6	0 620	_	_	_
Feb-03	0.234	1,5	0.649	0 743	1,5	0.428	0 042	1,5	0 846

Table 2.2 Summary of ANOVA for effect of microhabitat on number of freeze thaw cycles a), and hours spent below each threshold b) in a given month for *Grevillea* 2. June and July 2001 and June 2002 not analysed due to lack of sensor replication, _ indicates 0 cycles, or 0 hours spent below threshold. P values in red denote significant differences between microhabitats.

a)

	-0.5/0.5°C cycles			*-2.0/0.5°C cycles*			*-5.0/0.5°C cycles*		
	F	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
Aug-01	0.055	1,3	0.829	0	1,3	1	0.0857	1,3	0.789
Sep-01	4.983	1,4	0.089	1.8	1,4	0.251	4	1,4	0.116
Oct-01	7.2	1,3	0.075	0.019	1,3	0.898	_	_	_
Nov-01	1.516	1,5	0.273	5.714	1,5	0.062	_	_	_
Dec-01	0.333	1,6	0.5847	1	1,6	0.356	1	1,6	0.356
Jan-02	1	1,2	0.423	_	_	_	_	_	_
Feb-02	0	1,2	1	_	_	_	_	_	_
Mar-02	0.111	1,2	0.771	0.25	1,2	0.667	_	_	_
Apr-02	0.131	1,2	0.752	0.25	1,2	0.667	2	1,2	0.293
May-02	0.243	1,2	0.671	0	1,2	1	0.0118	1,2	0.924
Jul-02	0.375	1,4	0.573	0.069	1,4	0.806	0.2	1,4	0.678
Aug-02	0.441	1,3	0.554	0.475	1,5	0.521	0.1580	1,5	0.707
Sep-02	0.714	1,5	0.437	2.269	1,5	0.192	_	_	_
Oct-02	0.760	1,5	0.423	0.515	1,5	0.505	_	_	_
Nov-02	0.073	1,5	0.798	0.551	1,5	0.491	0.0311	1,5	0.867
Dec-02	0.765	1,5	0.422	2.286	1,5	0.191	_	_	_
Jan-03	1.946	1,4	0.235	1.8	1,4	0.251	_	_	_
Feb-03	2.574	1,4	0.184	0.25	1,4	0.643	_	_	_
Mar-03	1.052	1,5	0.352	0.025	1,5	0.881	1	1,4	0.374

b)

	-0.5/ 0.5°C hrs			*-2.0/ 0.5°C hrs*			*--5.0/ 0.5°C hrs*		
	F	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
Aug-01	0.100	1,3	0.772	0.075	1,3	0.802	0.003	1,3	0.959
Sep-01	13.154	1,4	**0.022**	0.040	1,4	0.851	3.449	1,4	0.137
Oct-01	0.008	1,3	0.936	0.262	1,3	0.644	_	_	_
Nov-01	5.230	1,5	0.071	3.197	1,5	0.134	_	_	_
Dec-01	0.442	1,6	0.531	1.190	1,6	0.317	1	1,6	0.356
Jan-02	1	1,2	0.423	_	_	_	_	_	_
Feb-02	0.576	1,2	0.527	_	_	_	_	_	_
Mar-02	0.017	1,2	0.909	0.088	1,2	0.795	_	_	_
Apr-02	0.244	1,2	0.670	0.218	1,2	0.686	0.234	1,2	0.676
May-02	0.074	1,2	0.811	0.115	1,2	0.767	0.047	1,2	0.849
Jul-02	0.155	1,4	0.714	1.046	1,4	0.364	0.373	1,4	0.574
Aug-02	0.714	1,3	0.437	0.363	1,5	0.573	0.103	1,5	0.761
Sep-02	0.216	1,5	0.662	3.040	1,5	0.142	_	_	_
Oct-02	1.171	1,5	0.329	0.263	1,5	0.630	_	_	_
Nov-02	0.319	1,5	0.597	0.692	1,5	0.443	0.013	1,5	0.912
Dec-02	1.260	1,5	0.313	1.437	1,5	0.284	_	_	_
Jan-03	1.008	1,4	0.372	5.488	1,4	0.079	_	_	_
Feb-03	0.909	1,4	0.394	0.962	1,4	0.382	_	_	_
Mar-03	0.422	1,5	0.545	0.105	1,5	0.759	0.524	1,4	0.502

Wind speed

Wind speed at 10cm above ground in bare patches was consistently higher than in the *Grevillea* canopy (Figure 2.17). The highest 20-minute mean wind speed recorded in *Grevillea* was 1.1 ms^{-1} (c. 4km/hr), while in the adjacent bare patch 4.5 ms^{-1} (c. 16km/hr) was the highest. These are certainly not the maximum speeds experienced in either of the microhabitats, as the thermoanemometers were not deployed during very strong winds in wet conditions. As a reference, Liawenee AWS recorded wind speeds of between 18 and 28 km/hr, with gusts reaching 31 to 42 km/hr in the same time period (Figure 2.18).

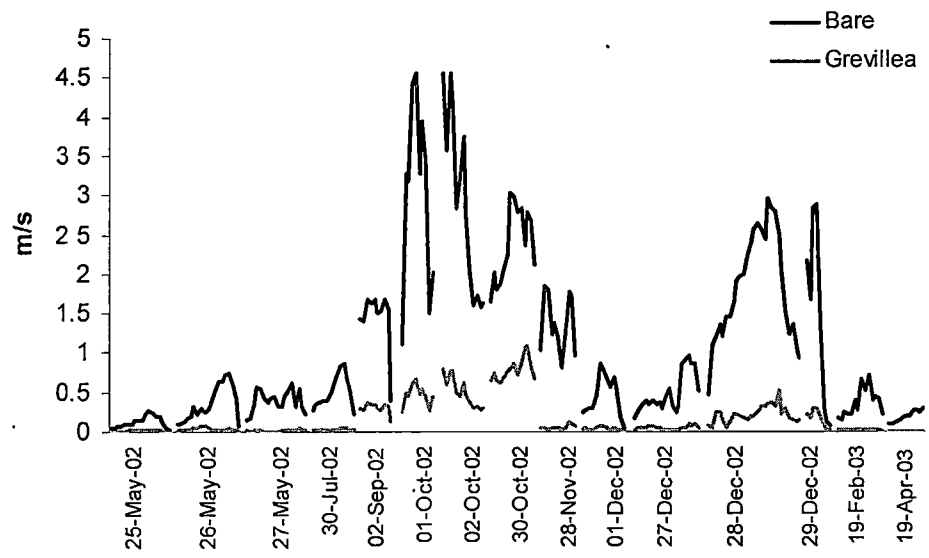


Figure 2.17 Near-ground level (10cm) wind speed in *Grevillea* shrubs and in adjacent bare patches at Liawenee Moore Exclosures.

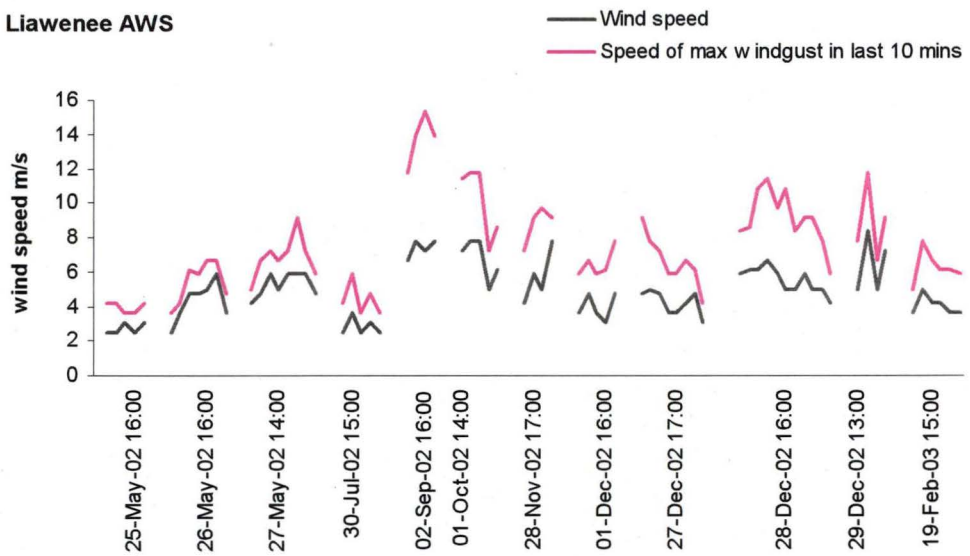


Figure 2.17 Hourly wind speed recorded at Liawenee AWS for periods covered by thermoanemometers. Note that data for some days is incomplete.

Solar radiation (PPFD)

Maximum PPFD levels were strongly seasonal and higher in bare areas than under *Grevillea* in winter, but not in late spring, summer and early autumn (Figure 2.18). Very low values indicate snow cover. Monthly integrated PPFD was consistently higher in bare patches than under *Grevillea* shrubs (Figure 2.19). January 2003 had the highest levels of integrated PAR (1242.36 mol m^{-2} in open ground and 856.81 mol m^{-2} under *Grevillea*), and July 2002 the lowest (247.84 mol m^{-2} in open ground and 117.81 mol m^{-2} under *Grevillea*). Daily maximum levels in open ground ranged from 29.5 μmol m^{-2} s^{-1} (11 September 2002) to 2451 μmol m^{-2} s^{-1} (6 December 2002), and under *Grevillea* from 3.4 μmol m^{-2} s^{-1} (6 July 2002) to 2345 μmol m^{-2} s^{-1} (4 January 2003).

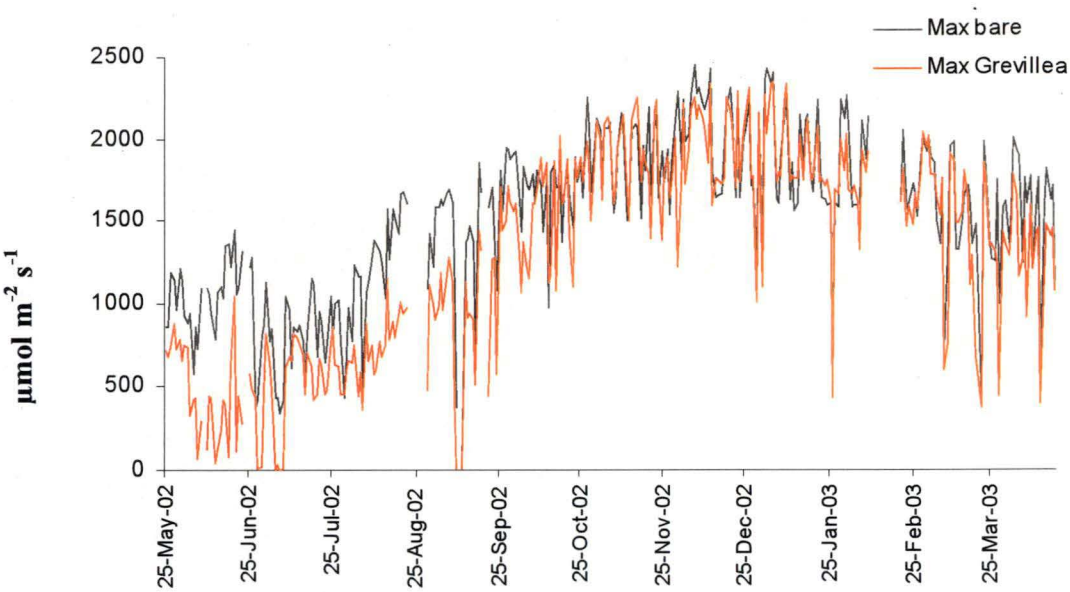


Figure 2.18 Daily maximum PPFD levels under *Grevillea* shrubs and in adjacent bare patches at Liawenee Moore Exclosures.

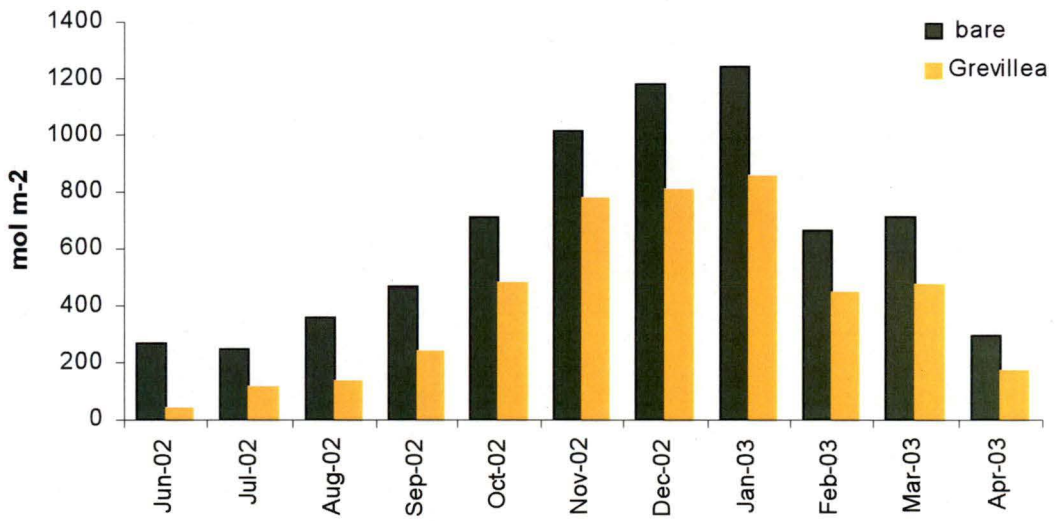


Figure 2.19 Integrated monthly PAR levels under *Grevillea* shrubs and in adjacent bare patches at Liawenee Moore Exclosures. (June 2002 missing 40 data points for *Grevillea*. August 2002 missing 7 days of data. April 2003 = 1st –17th only.)

Frost heave

Frost heave occurred throughout the year at all sites, except January and February 2002 and 2003. Mean VDG displacement was significantly higher in bare patches than under *Grevillea* for 74.1% of movements measured at the Exclosures ($F_{1,18}$ =56.32, P<0.0001) (Figure 2.21), 55.6% at Lake Augusta ($F_{1,8}$=12.24, P=0.008 and $F_{1,18}$=23.11, P=0.0001) (Figure 2.22), and 33.3% at Carter Lakes Carter Lakes($F_{1,\ 8}$=14.28, P=0.005) (Figure 2.23). Only mean VDG movement above 0.5 mm has been included in calculations and presented in the figures. The greatest mean frost heave registered by the VDGs was 27.75 (±1.97) mm at the Exclosures between 31 July and 28 August 2002 in bare ground. At Lake Augusta, 20.5 (±2.3) mm was the highest between 30 July and 30 August 2002, and at Carter Lakes 25.7 (±4.52) mm between 28 May and 27 July 2002. Individual VDGs however, could be heaved up to 38 mm in bare patches (Carter Lakes, between 28 May and 27 July 2002).

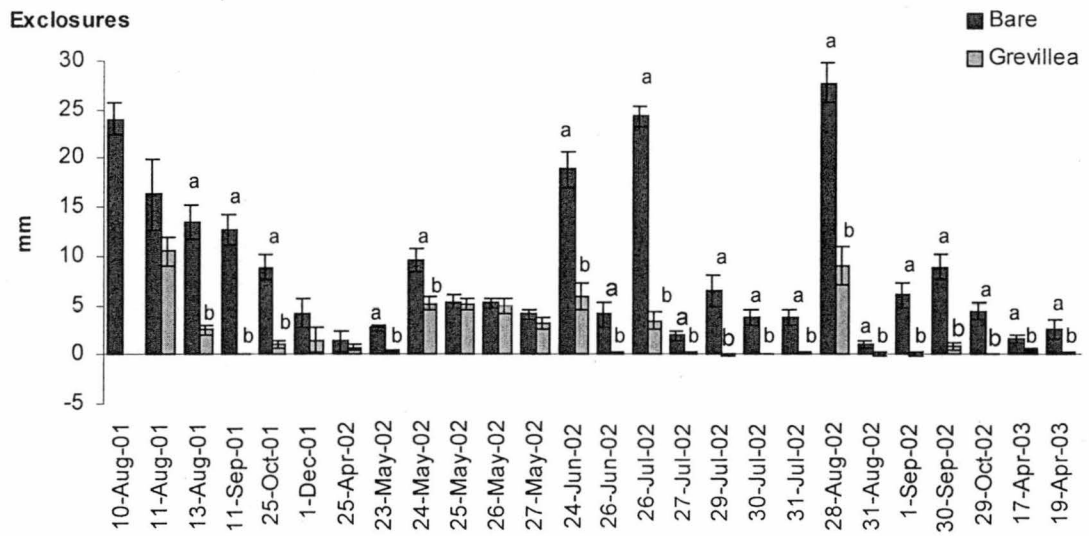


Figure 2.21 Mean soil frost heave under *Grevillea* shrubs (n= 2 - 10), and in adjacent bare patches (n= 6 - 10) at Liawenee Moore Exclosures. No data for *Grevillea* on 10 August 2001, while 0mm mean movement on 11 September 2001. Significant differences between bare and *Grevillea* VDGs (P<0.05) are denoted by different letters.

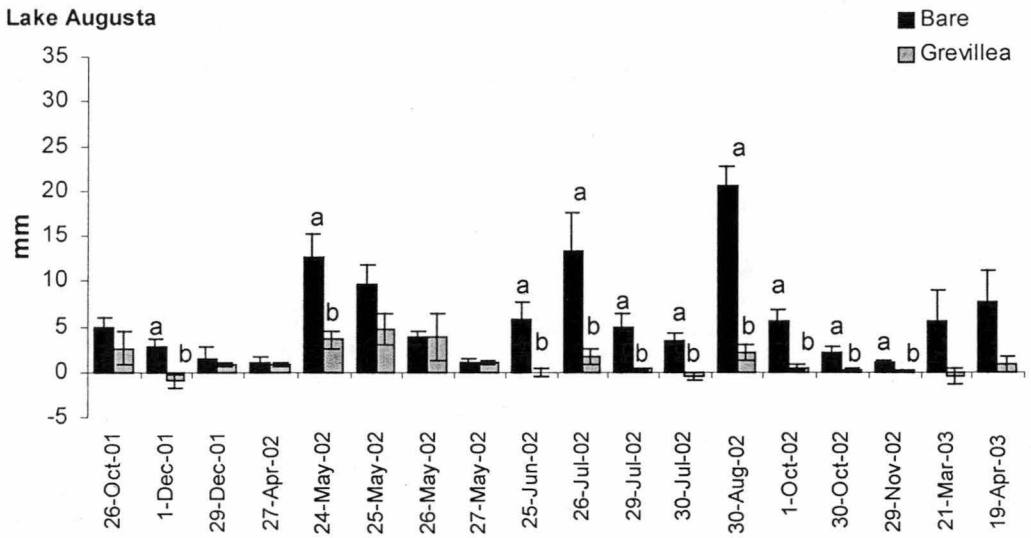


Figure 2.22 Mean soil frost heave under *Grevillea* shrubs and in adjacent bare patches at Lake Augusta (n= 5 – 10). Significant differences between bare and *Grevillea* VDGs (P<0.05) are denoted by different letters.

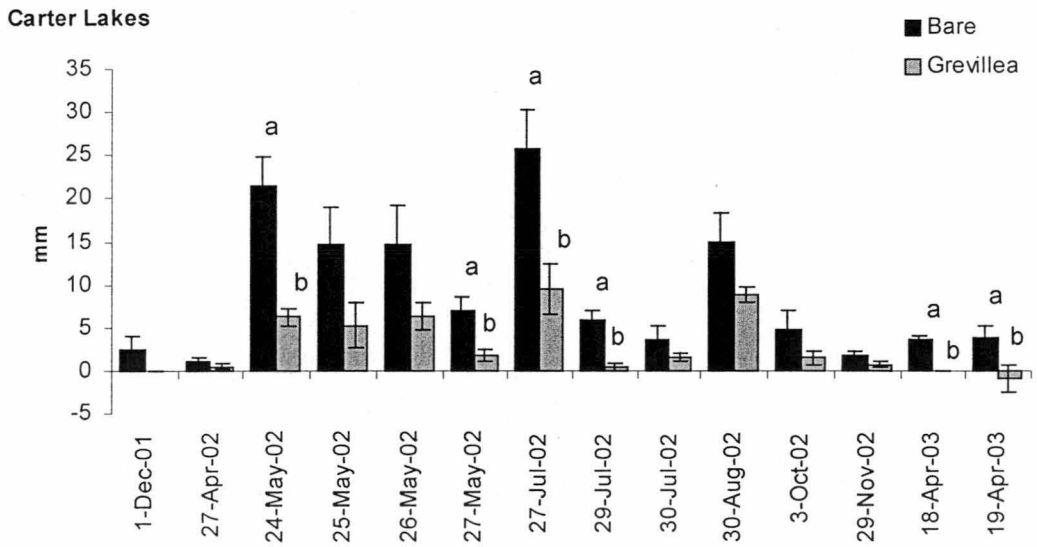


Figure 2.23 Mean soil frost heave under *Grevillea* shrubs and in adjacent bare patches at Carter Lakes (n= 5 - 8). Significant differences between bare and *Grevillea* VDGs (P<0.05) are denoted by different letters.

Bernacchi

Relative humidity (RH)

Relative humidity data at Bernacchi is fragmented due to only two sensors being available. Nevertheless, daily minimum RH was consistently higher under jute (17% to 71.5%, mean 36.9%) than in bare patches (between 11 and 61%, mean 27.4%) in early December 2002 (Figure 2.23). In mid-March and throughout September 2002, daily minimums were higher under slash (25 to 98.5%) than under jute (13.5 to 89.5%). The daily minimum RH in winter (July 2002) was persistently high under both jute and slash reflecting the high precipitation and snow conditions at that time of the year.

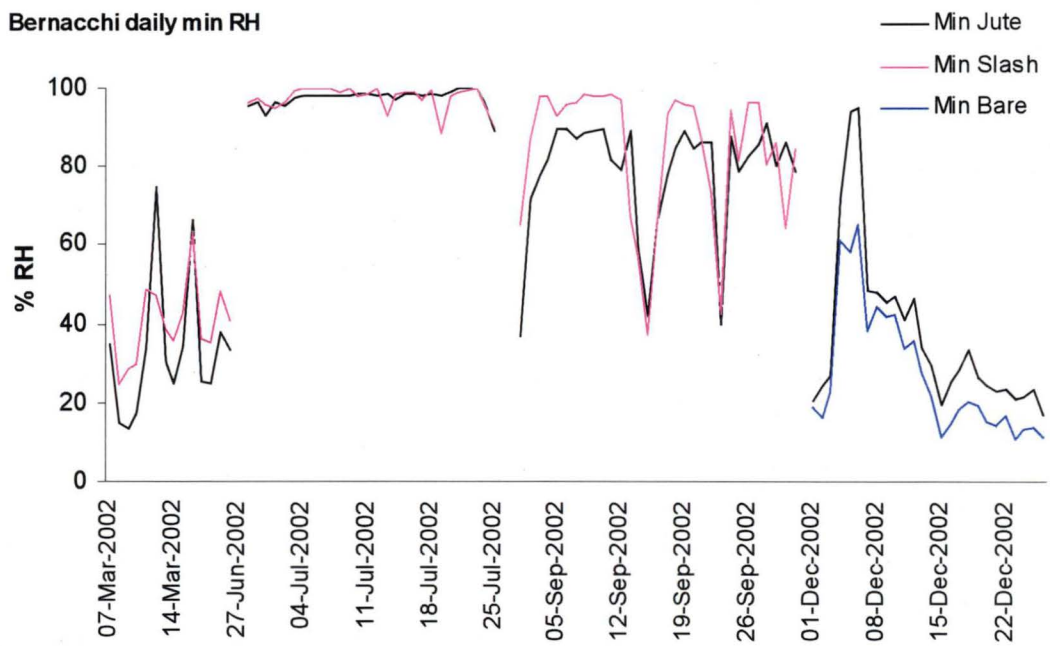


Figure 2.23 Daily minimum relative humidity under Jute, Slash and in adjacent bare patches at Bernacchi. Data from Vaisala sensors connected to Squirrel 32.

Surface air temperature

Mean daily minimum soil surface temperature throughout the time series was significantly higher under slash than under jute or in adjacent bare patches, and temperature under jute was also significantly higher than temperature in bare patches ($F_{3,2815}$=94.24, P<0.0001). Between April and November 2002 the daily minimum temperature remained largely below 0°C in all microhabitats (Figure 2.24 and Figure 2.25). During the rest of the year, it typically oscillated between 0 and 8°C, with the highest minimum of 13.7°C recorded under Jute on 30 December 2002. The lowest minimum recorded on the other hand was –13.1°C in a bare patch on 25 August 2002.

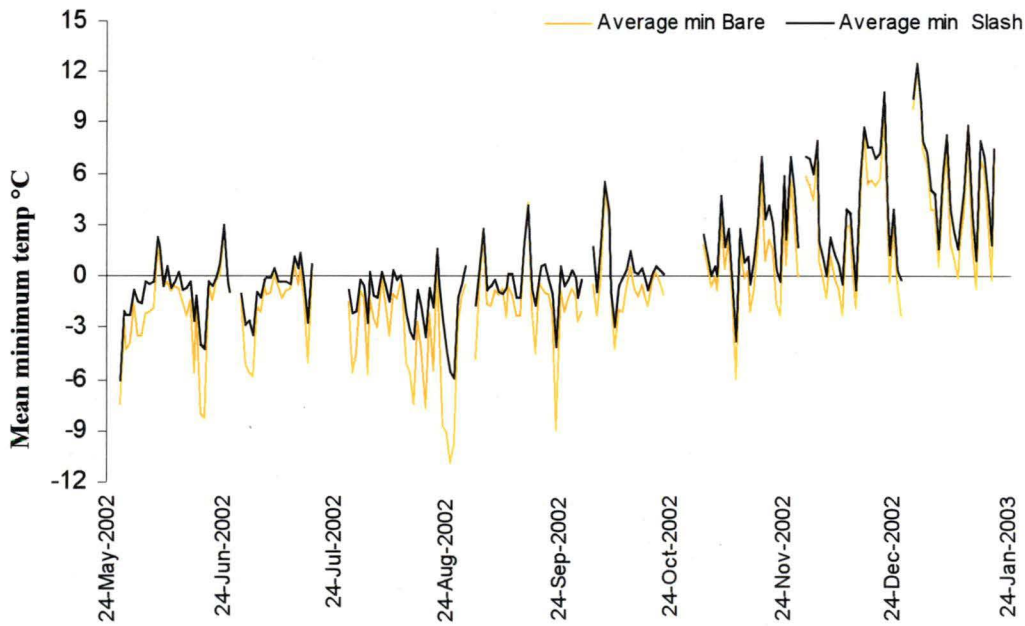


Figure 2.24 Daily minimum soil surface temperatures under slash and in adjacent bare patches. The values are a mean of 2 to 4 thermocouples logged by Squirrel 80.

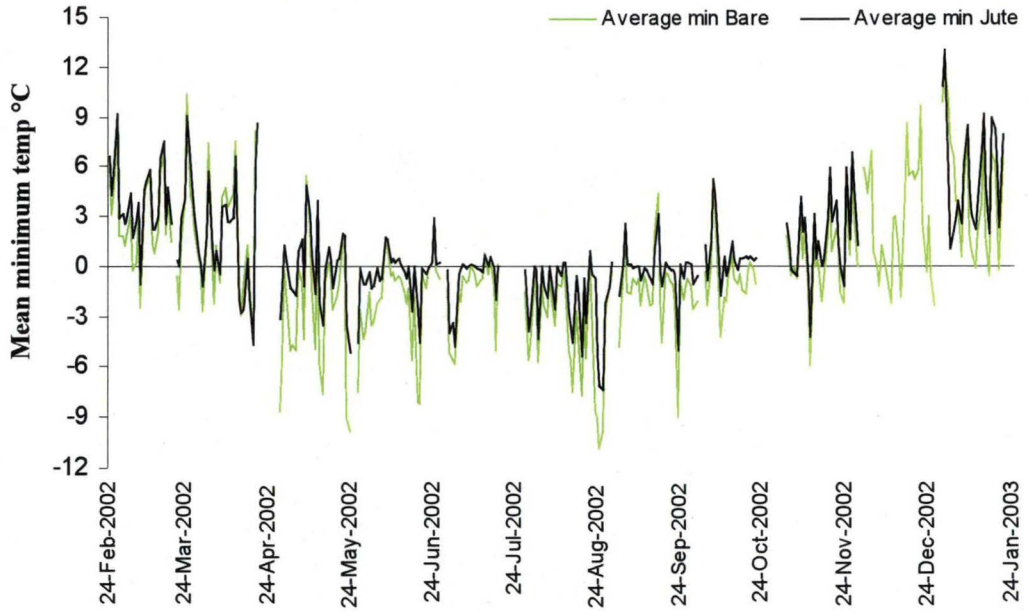


Figure 2.25 Daily minimum soil surface temperatures under Jute and in adjacent bare patches. The values are a mean of 2 to 4 thermocouples logged by Squirrel 80.

Freeze-thaw cycles

Mild freeze-thaw events (above -5°C) occurred throughout the year at Bernacchi, but more severe events (below -5°C) were not recorded in any microhabitat during January 2003 (Figure 2.26). In March and December 2002 only the vegetation clumps experienced temperatures below -5°C. In general, all freeze-thaw events were more frequent in vegetation clumps than in any other microhabitat at any time of the year, with May 2002 having the highest average of 32 cycles (±0.7). The longest time spent between the thresholds however, was in August 2002, indicating fewer cycles but more extended periods below –0.5/0.5°C in that month. If only the more severe freezing events are considered, vegetation clumps in May 2002 recorded both the greatest number of mean cycles (12 ±0.9) and the most hours spent between the –5/0.5°C threshold.

Microhabitat type had a significant effect on the number of freeze/thaw events and hours spent frozen below thresholds as shown by monthly data (Table 2.3). In May, July, and August 2002, freeze-thaw cycles were much more frequent in bare patches than in adjoining jute or slash areas. The difference was also significant for bare and jute microhabitats in October 2002, but not for slash and bare (Figure 2.27). These differences were also reflected in the number of hours spent between the –0.5/0.5°C threshold in those months, except in August 2002, where jute and bare did not differ (Figure 2.28). In addition, during September 2002, bare microhabitats remained frozen below the thresholds longer than areas under jute or slash, although the number of average freeze-thaw cycles was not significantly greater in bare areas that month. The more severe freezing events (below -5°C) followed a similar pattern to the –0.5°C threshold, but with no differences between any microhabitats in September or October 2002 for either cycles (Figure 2.27) or duration frozen (Figure 2.28), and with no significant difference in frequency of cycles between bare and jute in August 2002.

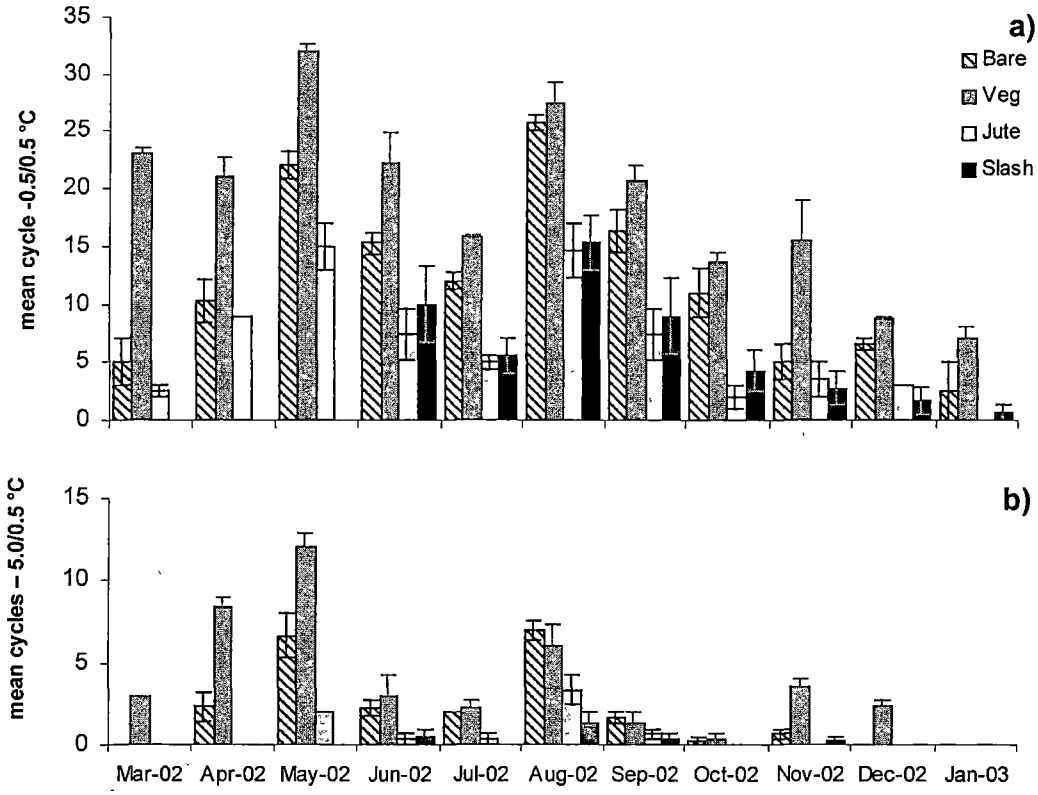


Figure 2.27 Mean monthly soil surface freeze–thaw cycles across a) - 0.5/0.5 °C, and b) – 5.0/0.5 °C threshold under Jute, Slash, in adjacent vegetation clumps and bare patches. The values are a mean of 2 to 4 thermocouples. Bars are ±1 SE.

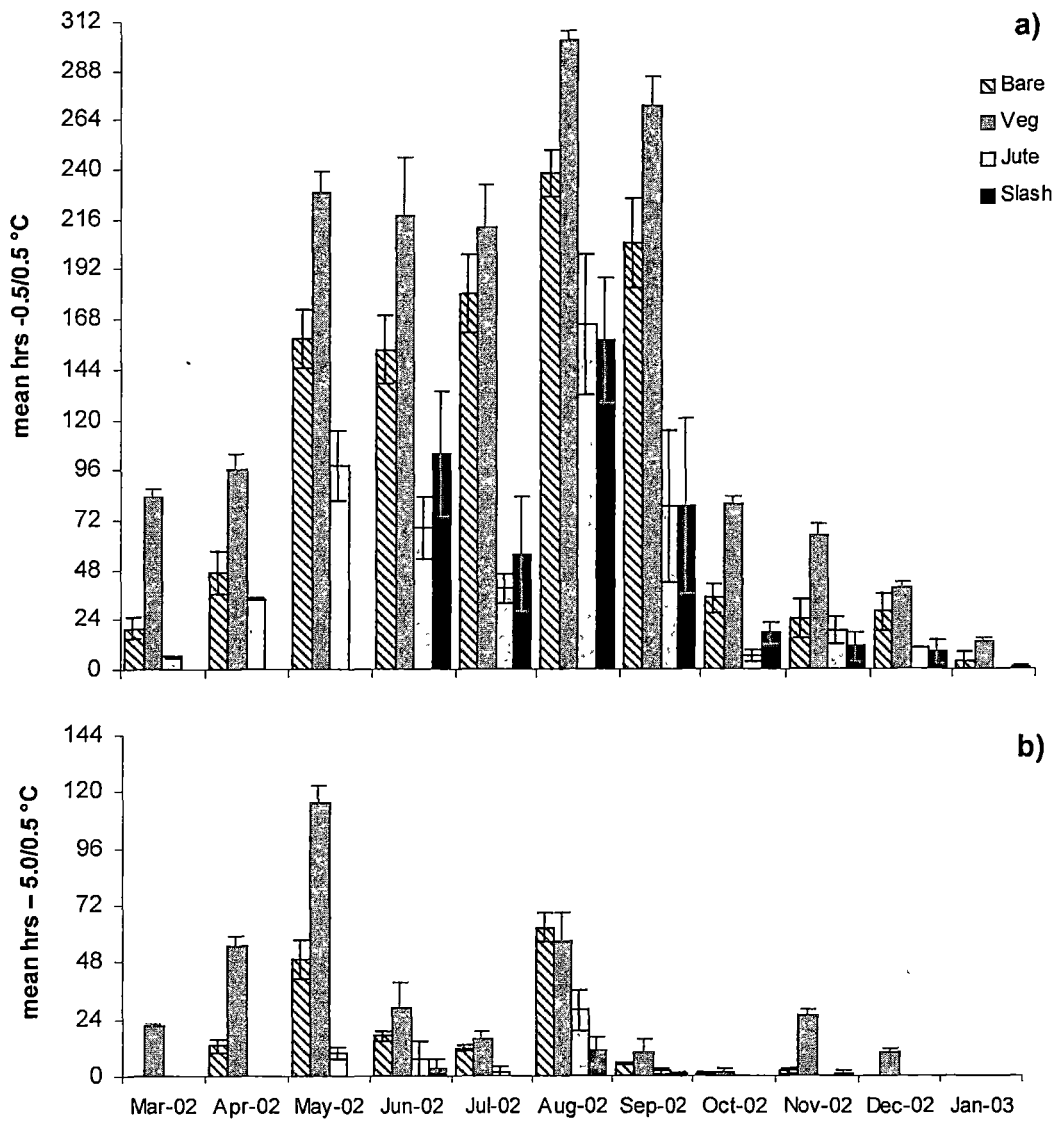


Figure 2.28 Mean monthly hours spent below the a) –0.5/0.5, and b) – 5.0/0.5 °C thresholds under Jute, Slash, in adjacent vegetation clumps and in bare patches. The values are a mean of 2 to 4 thermocouples. Bars are ± 1 SE.

Table 2.3 Summary of ANOVA for effect of microhabitat on number of freeze thaw cycles a), and hours spent below each threshold b) in a given month for Bernacchi. _ indicates 0 cycles, or 0 hours spent below threshold. P values in red denote significant differences between microhabitats.

a)

	-0.5/0.5°C Cycles			*-5.0/0.5°C Cycles*		
	F	**df**	**P**	**F**	**df**	**P**
Mar-02	122.19	2,4	0.0003	∞	2,4	<0.0001
Apr-02	15.34	2,5	0.0073	32.95	2,5	0.0013
May-02	57.67	2,6	0.0001	20.52	2,6	0.0021
Jun-02	7.08	3,11	0.0064	2.88	3,11	0.0842
Jul-02	58.86	3,9	<0.001	10.24	3,9	0.0029
Aug-02	13.62	3,10	0.0007	6.75	3,10	0.0091
Sep-02	7.58	3,8	0.01	1.90	3,8	0.2073
Oct-02	8.18	3,9	0.0061	0.58	3,9	0.6405
Nov-02	8.19	3,7	0.0109	56.93	3,7	<0.0001
Dec-02	10.16	3,6	0.0091	34.3	3,6	0.0004
Jan-03	6.01	3,4	0.0579	-	3,5	-

b)

	-0.5/0.5°C hours			*-5.0/0.5°C hours*		
	F	**df**	**P**	**F**	**df**	**P**
Mar-02	147.81	2,4	0.0002	197.84	2,4	0.0001
Apr-02	13.96	2,5	0.009	64.66	2,5	0.0003
May-02	23.2	2,6	0.0015	44.2	2,6	0.0003
Jun-02	6.69	3,11	0.0078	2.66	3,11	0.0996
Jul-02	19.63	3,9	0.0003	10.5	3,9	0.0027
Aug-02	11.72	3,10	0.0013	6.86	3,10	0.0086
Sep-02	9.76	3,8	0.0048	1.41	3,8	0.3096
Oct-02	24.95	3,9	0.0001	0.67	3,9	0.5905
Nov-02	7.47	3,7	0.0138	56.93	3,7	<0.0001
Dec-02	6.26	3,6	0.0281	36.28	3,6	0.0003
Jan-03	7.87	3,4	0.0374	-	3,5	-

Frost heave

The frost heave measurements at Bernacchi were limited due to the shallow soil and hence difficulty in anchoring the VDGs, nevertheless significant differences between microsites were recorded ($F_{3,12}$=81.25, P<0.0001). VDGs in bare patches were consistently heaved up the most, reaching a mean elevation of 50.25 (±15.25) mm

between 27 and 29 July 2002, which was significantly higher than VDGs under jute, slash or in vegetation patches (Figure 2.29). Displacement in bare patches was also significantly higher than under jute or slash on five other occasions, or a total of 40% of sampling days where movement above 0.5 mm was observed. The biggest individual movement recorded was 65.55 mm on a bare VDG between 27 and 29 July 2002. There was no significant movement (>0.5 mm) recorded on any of the monitoring occasions in the vegetation clumps. No displacement occurred in any microhabitat in January, February or March 2003.

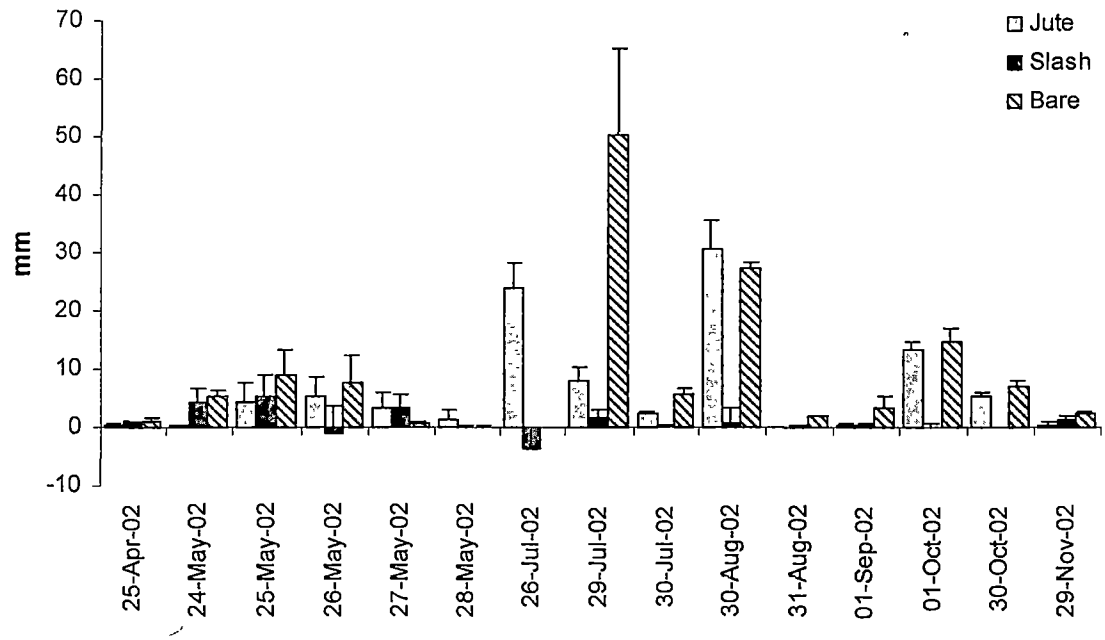


Figure 2.29 Mean soil frost heave in bare patches and under adjacent jute and slash at Bernacchi. Bars are ±1 SE.

DISCUSSION

Overall, the microclimatic parameters monitored at Liawenee exclosures show a predictable seasonal pattern of relative humidity and temperature at the soil surface, and reflect the larger scale patterns observed at the Bureau of Meteorology Liawenee AWS site, 2 km NW of the exclosures. Relative humidity is higher in the winter months, from May until November, when precipitation at the sites is also highest (see Table 1.1) with minimum temperatures during this period predominantly below 0°C. Much of April also experiences sub-zero minimum temperatures. Due to the increased moisture, frost heave during the cooler months is also more likely. As minimum temperatures climb above 0°C in November, moisture in the environment decreases. Such conditions present very limited opportunities for successful germination and seedling growth. Seedlings germinating with the onset of winter rains in April face low temperatures and frost heave, those that overwinter until spring or summer face drought. If seedlings are to survive long enough to establish, they will need a microhabitat that ameliorates these limiting microclimatic conditions. The understorey of *Grevillea* shrubs was assumed to be one such favourable microhabitat.

Frost heave data clearly supports the hypothesis that seedlings growing in bare patches are more likely to experience mechanical disturbance due to needle ice activity than those under *Grevillea.* Needle ice, leading to the bare soil surface being lifted and broken up to a depth of several centimetres, and to seedlings being wrenched out as well as the roots of existing plants being undermined has long been observed in areas of the Australian Alps affected by sheet erosion (Clothier & Condon 1968; Bryant 1971a), in high altitude snow tussock grasslands of New Zealand (Gradwell 1960), and in alpine and subalpine areas of southwestern British Columbia (Brink 1964). Leigh and others(1987) noted that needle ice can push seedlings, soil, and even stones up to 10 cm above the original surface. There has also been anecdotal reports of seedlings being heaved out by winter frosts of the Central Plateau (Mitchell 1962; Jackson 1973; Pemberton 1986; Richley 1986) Castro and co-workers (2004) observed *Pinus sylvestris* seedlings which have been lifted and loosened from the soil by frost heave, mostly in

open, bare soil microhabitats in a Mediterranean community in southern Spain (Sierra Nevada National Park), and mortality of *Calluna vulgaris* seedlings was largely due to disturbance from needle ice in unconsolidated peat following fire in North York Moors (Legg *et al.* 1992). Anderson and Bliss (1998) also noted up to 32% of adult plants were heaved out in bare soil patterned ground microsites in a Devon Island polar desert. In that particular landscape, cryptogamic crusts prevented the ejection of seedlings and adults, and rocks in sorted nets and stripes also stabilized the soil conditions and were associated with seedlings and adult plants. Rocks and cushion plants have also been observed to be important seedling refugia in the Andean paramo, providing protection from frost heave (Pérez 1987). In some bare patches on the Central Plateau such microtopographic features are scarce, suggesting that seedling establishment is unlikely to occur away from gap borders.

The extent and frequency of frost heave differed between sites however. This could be attributed to measurements on different days at different sites, as well as varying number of replicates and soil type and moisture content. Jumpponen *et al.* (1999) observed needle ice forming mostly on silt surfaces, but not where pebbles and gravel provided surface cover. Coarse, sandy soils do not hold water as well as soils with high silt and organic mater content, and are not as conducive to rapid migration of soil moisture to the freezing plane, thus arresting needle ice growth (Gradwell 1960; Outcalt 1971; Pérez 1987). Matsuoka (1996) found that diurnal frost heave up to 3cm frequently took place during spring and autumn on Mt Ainodake, c. 3000m a. s. l., but that soil moisture rather than the intensity of freezing was the primary control.

Another consequence of soil loosened by this disturbance is the increased susceptibility to being transported by wind or water, further promoting erosion and making it impossible for bare areas to stabilize naturally (Pérez 1987). Desiccation is also likely to be promoted by the higher wind speeds recorded in open areas. In addition, seeds deposited in bare patches are more likely to be moved along the ground or be picked up by wind gusts, whereas very low wind speeds in the *Grevillea* canopy are unlikely to further displace any seeds.

Light levels were also much higher in bare areas, particularly in winter and spring, and similar to those reported in other high altitude environments on the Australian mainland (Egerton *et al.* 2000). Coupled with low temperatures at this time of the year, any seedlings persisting in those exposed areas could face periods of photoinhibition stress. Sheltered snow gum (*Eucalyptus pauciflora*) seedlings grown at a similar elevation in Namadgi National Park, ACT, have been reported to be less photoinhibited and have higher photosynthetic CO_2 assimilation rates than exposed seedlings lacking nurse plants (Egerton *et al.* 2000). The total monthly amounts of PAR are also higher in bare areas throughout the year, and could be an advantage to a growing seedling during favourable temperature and moisture conditions.

Conversely, relative humidity results are in contrast to some predictions made at the outset of this study. Although higher daily minimum relative humidity was recorded under *Grevillea* than in the open at one location, there were no differences between bare ground and *Grevillea* microhabitats at the other location being monitored. While this discrepancy between the two loggers could be a sensor error, it is also possible that these differences are shrub or location specific. In the absence of replicate humidity probes under the same *Grevillea* the question remains unresolved. All sensors were tested in the laboratory prior to being deployed in the field and the readings obtained did not indicate any problems with the electronic equipment. The two Grevilleas chosen for monitoring were some distance apart, and their position in the landscape could have affected their microclimate. It is also possible that the orientation of the PVC shields over the sensors allowed varying amounts of sunlight to reach and dry the sensors to different extents. Under this scenario though, the maximum values, which were usually reached at night should not be affected, and show no differences between bare ground and *Grevillea* readings. This was not the case, with daily maximum relative humidity also higher under *Grevillea* than in the bare patches at one location but not the other.

This discrepancy in data between the two loggers was not encountered with daily minimum temperature measurements. Unlike the case with relative humidity however,

both Squirrels used the same type of sensors. Once again, contrary to expectations, there were no clear differences in the mean values between *Grevillea* and open ground. This was also reflected in the frequency of freeze-thaw cycles per month being similar in both microhabitats. Surface temperatures remained below 0°C for about a quarter of the month during May, June, July and August 2002 in both open areas and under *Grevillea.* Compared to similar microclimatic data from another environment which experiences diurnal frost action, the Western Cape mountains of South Africa, c. 1900 m a.s.l. (Boelhouwers 1998), the Central Plateau experiences more frequent and more intense frost at the soil surface, as well as a longer frost season. Boelhouwers' (1998) data emphasises the high interannual variability in the number of freeze thaw cycles observed, which is also evident in the present study, with substantially more freeze-thaw events in August 2002 than 2001.

Due to problems with the daily maximum temperature data, it was not used to compare microhabitats, but it could be in this portion of the temperature spectrum that differences between open and sheltered habitats are most pronounced, and are crucial to seedling performance. Henriquez & Lusk (2005) found *Empertatum rubrum*, a prostrate shrub, to facilitate the establishment of *Nothofagus antarctica* seedlings in a Patagonian glacial moraine, and speculated this was mainly as a result of more favourable temperature conditions under the shrub canopy. Mean daily maximum temperature at 2 cm above ground was significantly lower during summer and higher during winter under the canopy of *E. rubrum* than outside, while mean daily minimum temperature was significantly higher both in winter and in summer. However, the absence of replicate shrubs or sensors within each microenvironment means that it is not certain whether these results reflected universal differences across the general *E. rubrum* population.

It is likely that differences in temperature and humidity between *Grevillea* and bare patches do exist, but those environments are not themselves homogeneous and smaller scale, microsite differences occur within them, as illustrated by the range of temperatures recorded in both microhabitats. If only the Rotronic sensors data is examined, freeze thaw cycles were more frequent in that particular bare microsite than

under a corresponding *Grevillea* microsite every month. The thermocouple wire is very uniform in composition; consequently there is very little variation between individual thermocouples (Pearcy *et al.* 1989), so the differences in temperature are a result of microsite differences rather than sensor calibration. Although averages were presented here, it is the extreme conditions in these individual microsites that could be more important. Furthermore, a critical number of these microsites might need to be sampled to establish differences between *Grevillea* and bare patches in general. Two replicates per treatment for some of the time series presented here are likely to be inadequate. This kind of high within-microhabitat (microsite) abiotic heterogeneity under shrubs was also observed by Gomez-Aparicio and colleagues (2005) and Forseth and co-workers (2001), and is related to leaf size and shrub architecture.

The prostrate forms of *Grevillea* encountered on the Central Plateau are analogous to other ground covers utilised in geoconservation work, with a similar aim of stabilising soil and ameliorating eroded surfaces for seedling establishment. Both jute matting and slash composed of native vegetation have been used for this purpose (Clothier & Condon 1968; Comfort 1999, 2000). Each material has varying labour cost, accessibility and longevity, so being able to quantify which one provides potentially more favourable conditions for vegetation re-establishment could be very desirable in terms of management strategies for degraded areas. From the data obtained at Bernacchi, jute quite clearly maintained higher minimum relative humidity than eroded patches, but *Orites acicularis* slash appeared to outperform jute in this respect on most days for which data was available. Although both jute and slash maintained higher daily minimum temperatures than those in bare, slash was significantly warmer than jute. However, when it comes to the frequency of freeze-thaw events or the length of time below the freezing thresholds, both jute and slash appear to be equally effective in ameliorating those conditions in eroded areas. Slash and jute also appear to reduce frost heave on equal number of occasions, but jute tended to be heaved higher. *Grevillea* shrubs were not monitored at this site, which is approximately 100 m higher than Liawenee Moor, and could be influencing temperature and humidity in a similar way to jute matting or slash.

This study presents up to 24 months of largely continuous monitoring of microclimate parameters in open and sheltered habitats, and is the first relatively long-term investigation of soil surface temperature, relative humidity, wind speed, solar radiation and soil frost heave in an Australian alpine system. Although jute matting and *Orites acicularis* slash ameliorate the low temperatures recorded in the open, *Grevillea* shrubs do not appear to affect minimum temperatures at another site in the same way, and relative humidity differences are not clear either. The amount of soil frost heave however, was substantially greater in open areas than under shrub canopies, despite the number of freeze-thaw cycles, and the number of hours below freezing thresholds being similar in both microhabitats. On the other hand, freeze-thaw cycles were more frequent, with more hours below freezing in bare patches than under jute or slash for several months of the year. *Grevillea* shrubs did attenuate solar radiation and wind speed, potentially reducing photoinhibition and desiccation damage to seedlings. Although in general *Grevillea* is likely to play an important nurse-plant role for establishing seedlings, there is high abiotic heterogeneity at the within-microhabitat scale, and a more detailed and focused microclimatic investigation is warranted. There is no doubt however, that protection from frost heave and needle ice action offered by *Grevillea* canopies is of crucial advantage for seedling survival, regardless of the variability of other parameters.

Chapter 3. Seedling survivorship

INTRODUCTION

Recruitment depends on the interaction between seed dispersal and safe site availability for seedlings. Microsites must not only successfully trap seeds, but also support germination and seedling establishment. However, a good microsite for seed interception or emergence might not be equally favourable to seedling establishment and growth, so called seed-seedling conflict (Steenbergh & Lowe 1969; Franco & Nobel 1988; Wood & Morris 1990; Chambers 1995b; Aguiar & Sala 1997; Titus & del Moral 1998; Rey & Alcántara 2000). Neighbours can provide safe sites for seedling emergence and establishment by providing a buffer from environmental extremes, but they can also compete for resources. Positive and negative plant interactions can occur simultaneously and the balance between facilitation and competition can depend on the species involved, or shift with life stages and the extent of abiotic stress (Franco & Nobel 1989; Callaway & Walker 1997; Ibáñez & Schupp 2001; Klanderud & Totland 2005). In general, facilitation increases in stressful environments, while the balance shifts to competition under more favourable mesic, low elevation or sheltered conditions (Callaway & Walker 1997; Choler *et al.* 2001; Callaway *et al.* 2002; Arroyo *et al.* 2003; Olofsson 2004). In environments where extreme cold or heat restricts the ability of plants to acquire resources such as light, water and nutrients, any amelioration of these stresses by neighbouring plants is likely to have a greater benefit for growth than competition for resources is likely to be of detriment (Callaway *et al.* 2002).

Established individuals that provide a more favourable environment for seedlings, or "safe sites", are frequently referred to as "nurse plants" (Steenbergh & Lowe 1969). Facilitation by nurse plants may be due to reduced temperature, increased moisture retention and nutrient availability, or protection from herbivory and physical disturbance caused by hazards such as trampling, hailstorms, wind damage or frost heave (Carlsson

& Callaghan 1991; Choler *et al.* 2001). These interactions are important in structuring plant communities, as the dominant species is often vital in driving ecosystem function and community dynamics. The less stress-tolerant species, or those at the limit of their range are most likely to be facilitated by the more dominant, stress-tolerant species in a particular community and as a result, facilitation can act to increase the biological diversity of severe environments (Kikvidze & Nakhutsrishvili 1998; Choler *et al.* 2001). The nurse plant syndrome has been widely described for many systems, including arid and semi-arid environments (Steenbergh & Lowe 1969; Franco & Nobel 1988, 1989; Brittingham & Walker 2000), Mediterranean mountains (Castro *et al.* 2004; Gómez-Aparicio *et al.* 2005), as well as tundra, subnival and alpine communities (Carlsson & Callaghan 1991; Kikvidze & Nakhutsrishvili 1998; Nuñez *et al.* 1999; Arroyo *et al.* 2003; Klanderud & Totalnd 2004; Olofsson 2004; Cavieres *et al.* 2006) and glacial moraines (Henriquez & Lusk 2005). However, little is known about seedling dynamics and re-colonization of gaps formed by disturbance in Tasmanian alpine environments dominated by shrubs.

One of the widespread and dominant shrub species on the Central Plateau, *Grevillea australis,* has been observed to play a major role in stabilising eroded areas in alpine heath communities (Pemberton 1986; Bridle 1987; Cullen 1995). The prostrate form of this shrub grows laterally c. 5-10 cm a year, (Bridle 1987; Cullen 1995), but is sensitive to trampling (Whinam *et al.* 1994; Whinam & Chilcott 1999). This study aimed to evaluate the potential role of the prostrate form of *Grevillea australis* as a nurse species for seedlings on the Central Plateau, where the patchy structure of the vegetation and severe abiotic conditions create well-differentiated microenvironments. In particular, the following two questions were considered:

1. Are seedlings aggregated under the shrub's prostrate canopy in contrast to limited recruitment in adjacent open microhabitats?
2. Does the pattern of seedling distribution vary seasonally, i.e. is *Grevillea* microhabitat less or more important in providing safe sites for recruitment at certain times of the year?

The possible biotic and abiotic reasons behind facilitation are also discussed.

METHODS

Seedling transects

In late February and late March 2001, a number of transects was established from underneath *Grevillea* canopies out into bare soil gaps at Liawenee Moor Exclosures, Carter Lakes, and Lake Augusta sites (see Chapter 1 for site descriptions). All prostrate Grevilleas of adequate size were sampled in both exclosures at Liawenee Moor, and all suitable Grevilleas within relatively homogenous vegetation at the other sites. The transects were 20 cm wide and divided into 25 cm long contiguous quadrats. Only plants with a minimum canopy of this size (c. 20 x 25cm) were selected. Some transects extended up to two meters in length, but the majority were limited to 1.5 m. A single *Grevillea* plant usually supported between one and five transects. The proximity of transects within individual shrubs varied. The start of the transects could converge within centimetres of each other, but as they headed in different compass direction, the distance could increase to several meters at the final quadrats. Individual Grevilleas were usually several meters apart.

The number of seedlings was counted in each quadrat and if possible, identified to species or family level. The term "seedling" as used here includes individuals at the cotyledon stage and young plants with 1 –2 pairs of expanded leaves, or "juveniles". Height was not a deciding factor due to the variety in habit of some species, e.g. rosette herbs, monocotyledons, slow growing shrubs. In general, very few adults were present in the transects. Adults were censused on two occasions, in February 2001 at Carter Lakes, and March 2001 at Carter Lakes and Lake Augusta (data not presented). Recording adults was problematic, as often it was difficult to distinguish individuals aggregated in clumps (especially grasses and graminoids), or possibly spreading vegetatively, for example *Coprosma* sp. and was therefore abandoned in later surveys.

Grevillea cover was also estimated in each quadrat to the nearest five percent. The start of the transect was placed as close as possible to the *Grevillea* stem to sample at least one section (0 – 25 cm) with 100% cover (Figure 3.1). Metal pegs with a numbered tag

and compass direction of the transect were used to relocate the same area for subsequent surveys.

Figure 3.1 Seedling transect extending from base of *Grevillea* stem to adjacent bare patch.

The transects were re-sampled between 13 and 23 February 2002, and new transects were established at Lake Botsford. Seedling counts were repeated between 25 April and 24 May 2002 at the Exclosures, on 27 May 2002 at Lake Augusta, and at Carter Lakes between 27 May and 30 July 2002. The Lake Botsford transects were re-visited between 31 August and 2 September 2002. The autumn/winter census was staggered over four months due to cold, wet and windy conditions, with snowfall preventing work during a June 2002 trip. All transects were again re-sampled at the end of December 2002, and those at Carter Lakes, Lake Augusta and Lake Botsford were also visited between 18 and 21 April 2003. Although the majority of transects were easily located from season to season, some were discarded due to *Grevillea* branch damage and death, or to markers being heaved out by frost action, or displaced by animals. In most cases, new transects

were established to replace the original ones. Consequently, the location and number of transects varied to some extent between census dates. On each occasion, between 21 and 24 transects distributed among 15 to 20 *Grevillea* plants were surveyed at the Liawenee Moor Exclosures, nine transects within three *Grevillea* at Lake Augusta, 21 to 27 transects within 13 *Grevillea* at Carter Lakes, and 41 transects within 28 *Grevillea* were sampled at Lake Botsford.

Data analysis

Seedling data was analysed using GLM procedures in SAS ver.9.1 (SAS Institute Inc. 2002). As it was not logistically achievable to census all sites at the same time, a single analysis including all sites and all dates was impossible. Therefore, seedling density and cover were analysed at each census time separately using a 2-factor ANOVA with site and transect section as the two fixed factors, with individual transects as replicates. Since there was a significant site x transect section interaction, data were re-analysed by site, using a single factor ANOVA with transect section the single fixed factor. Secondly, data was re-analysed for each site separately using a 2-factor ANOVA with census time and transect section as the two fixed factors. This approach allowed comparisons among sites at a particular census date where possible, and to separately assess temporal patterns in seedling density within a site.

Within-site differences for each census date, and seasonal changes in seedling density along the transects, as well as between-site differences for February 2002, December 2002 and April 2003 were compared *post hoc* with the Ryan-Einot-Gabriel-Welsh Multiple Range Test (Day & Quinn 1989). Due to the extended time it took to census all sites in February/March 2001, and April to September 2002, the data collected could not be used for between-site comparisons for those periods. Census dates for February 2002 were a maximum of 12 days apart, 3 days for December 2002, and 4 days for April 2003.

RESULTS

More seedlings were present under *Grevillea* canopies than in adjacent bare quadrats ($P<0.0001$) for all sample periods, at all sites, except February 2001 at the Exclosures (Table 3.1), when very low numbers of seedlings were recorded in all quadrats (Figure 3.2 and Figure 3.3). In contrast, February 2002 had the highest seedling numbers of any census period at all sites. The highest average number of seedlings recorded in a 20 x 25 cm quadrat under *Grevillea* was 18.04 (±2.05), or 360.8 (±41) seedlings/m^2 in February 2002 at the Liawenee Moor Exclosures, and the lowest was 2.03 (±0.53), or 40.6 ±10.6 seedlings/m^2 in February 2001, also at the Exclosures. In bare gaps, the highest average number of seedlings was 108 ±58.2/m^2 in February 2002 at Carter Lakes, with a mean of nil seedlings recorded in many sections on multiple occasions.

Table 3.1 Results of analysis of variance of the effect of distance from the base of *Grevillea* on seedling densities for each census period at each site. NS, non-significant; -, analysis not possible.

	Feb/Mar 2001	Feb 2002	Apr-Sep 2002	Dec 2002	Apr 2003
Lake Botsford	-	*P<0.0001* $F_{5,181}=20.47$	*P<0.0001* $F_{5,180}=16.18$	*P<0.0001* $F_{5,182}=19.41$	*<0.0001* $F_{5,175}=13.61$
Carter Lakes	*P<0.0001* $F_{6,105}=10.35$	*P<0.0001* $F_{5,120}=7.53$	*P<0.0001* $F_{5,120}=28.23$	*P<0.0001* $F_{5,122}=37.48$	*P<0.0001* $F_{5,110}=22.02$
Exclosures	*NS* $F_{7,160}=1.52$	*P<0.0001* $F_{5,106}=22.32$	*P<0.0001* $F_{5,112}=18.82$	*P<0.0001* $F_{5,109}=9.62$	-
Lake Augusta	*P<0.0001* $F_{4,33}=8.85$	*P=0.01* $F_{4,35}=3.89$	*P=0.007* $F_{4,36}=4.18$	*P<0.0001* $F_{4,37}=11.92$	*P=0.0003* $F_{4,37}=6.80$

Seedling densities in quadrats at the *Grevillea*/bare patch boundary, usually at 25-50 cm along the transect, generally reflected the relatively low canopy cover in those sections (Figure 3.4). In all of the 25-50 cm quadrat surveys at Lake Augusta, and in over half at Carter Lakes, Lake Botsford and Liawenee Exclosures, *Grevillea* cover was less than 50% (Figure 3.3). Typically, there were fewer seedlings here than under full *Grevillea*

canopies closer to the shrub stem (Figure 3.2 and Figure 3.3), with numbers comparable to those in bare areas (all dates at Lake Botsford, March 2001, December 2002 and April 2003 at Lake Augusta, December 2002 at Carter Lakes, and April/May and December 2002 at the Exclosures). Occasionally, average seedling densities in quadrats with variable cover levels were significantly lower than under full *Grevillea* canopies, but higher than in bare gaps (February 2002 at the Exclosures, and May/July 2002 and April 2003 at Carter Lakes), or intermediate between *Grevillea* and bare quadrats (February/March 2001 and February 2002 at Carter Lakes, and February and May 2002 at Lake Augusta), an indication of the uneven *Grevillea* cover in these sections. The relationship between *Grevillea* canopy cover and seedling density was tested with simple linear regression for all sites and sample times and well as for separate census periods, but no significant correlation was revealed.

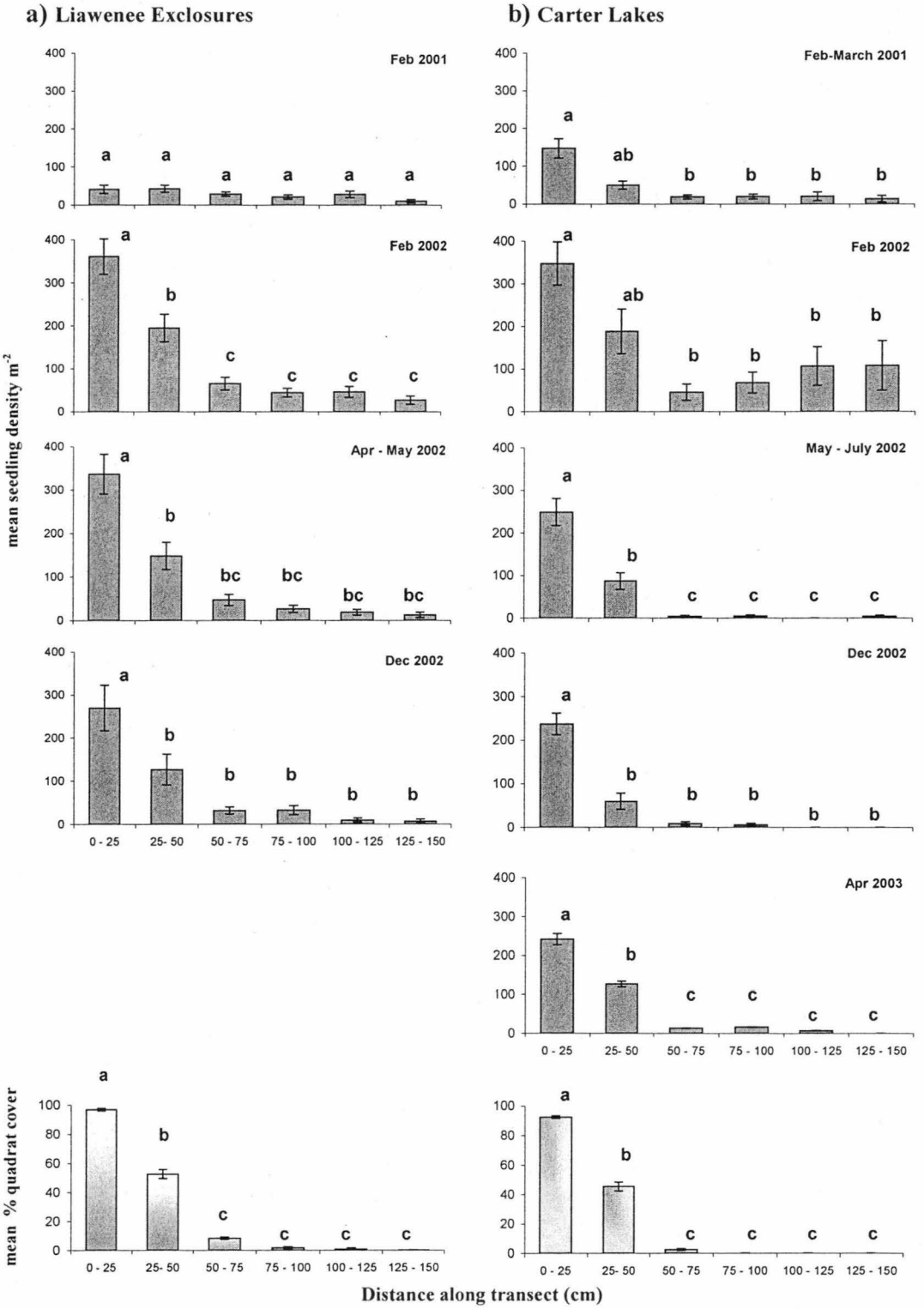


Figure 3.2 Mean number of seedlings along *Grevillea* transects and mean *Grevillea* cover along transects at a) Exclosures and b) Carter Lakes. Significant between-transect section differences ($P<0.05$) are denoted with different letters.

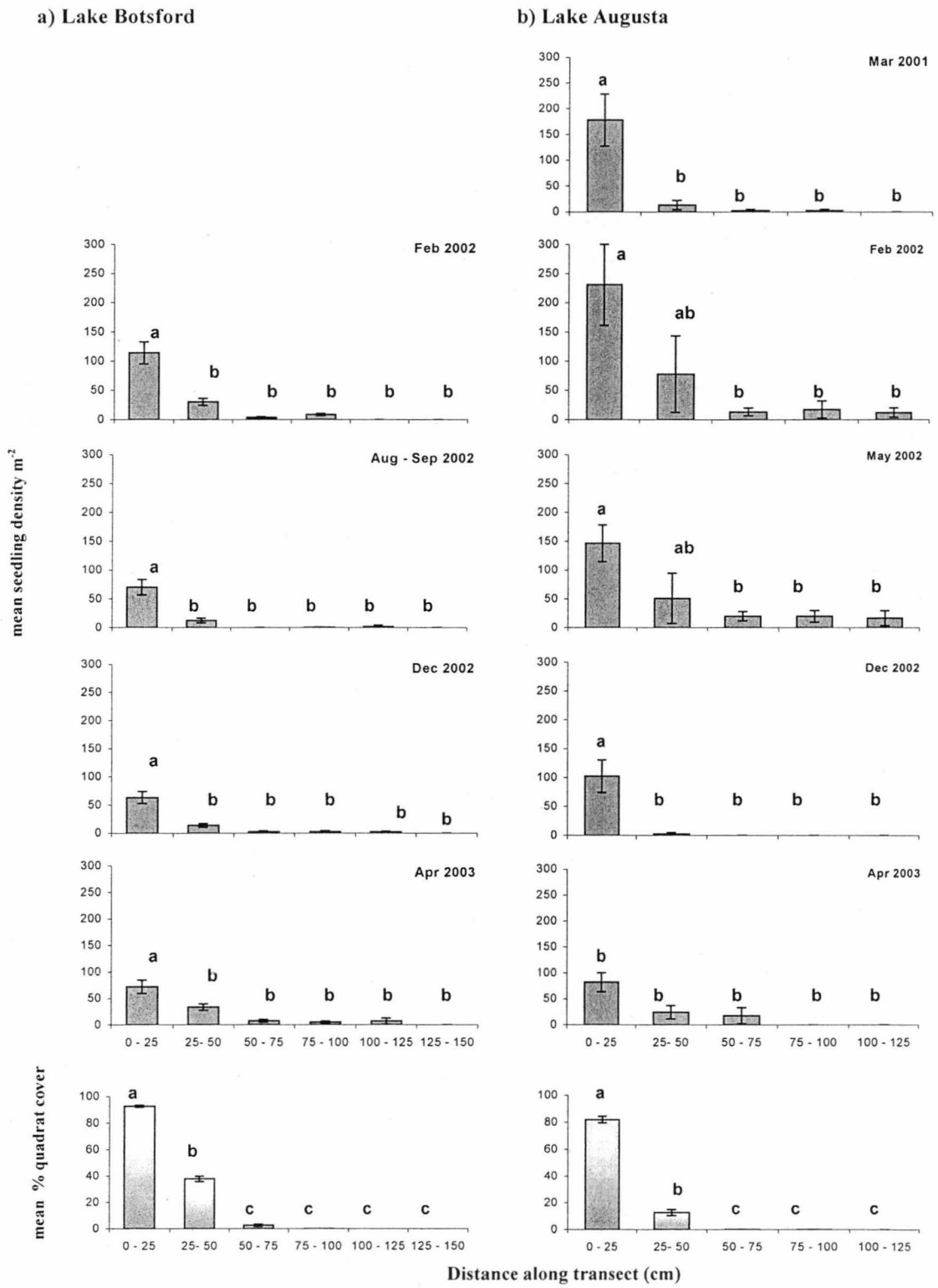


Figure 3.3 Mean number of seedlings along *Grevillea* transects and mean *Grevillea* cover along transects at a) Lake Botsford and b) Lake Augusta. Significant between-transect section differences ($P<0.05$) are denoted with different letters.

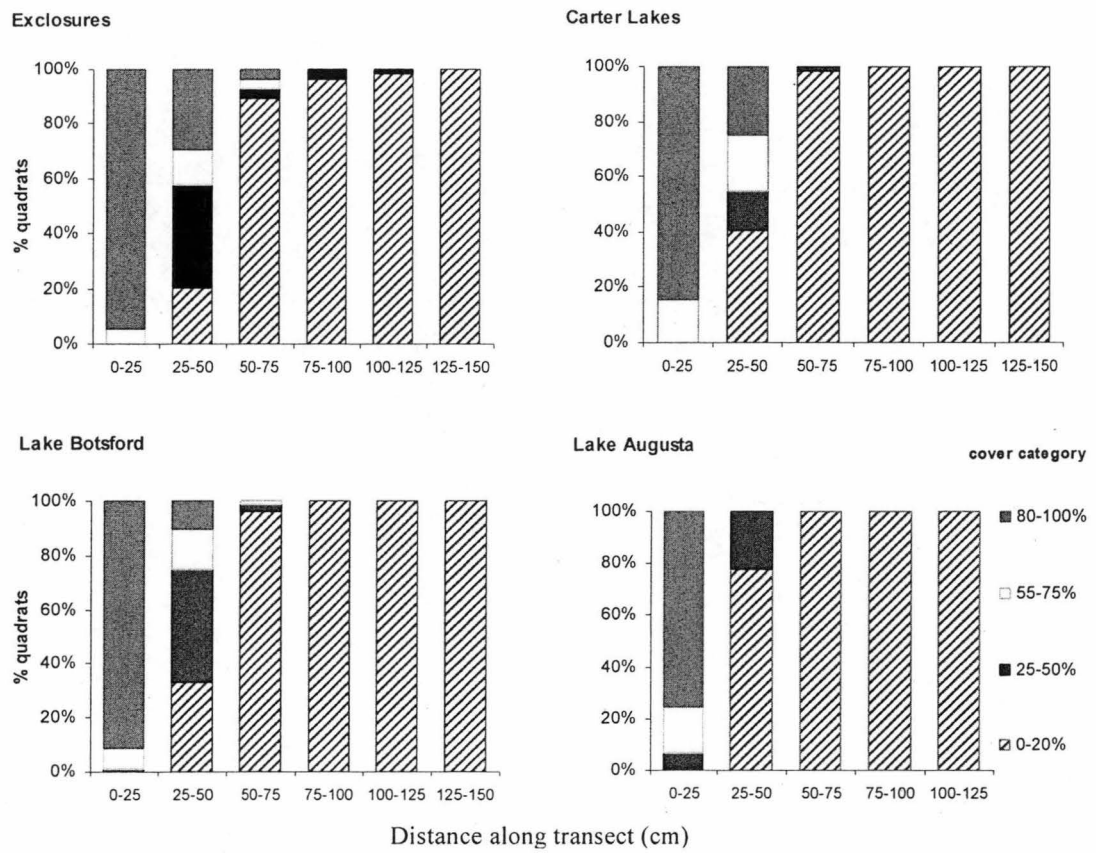


Figure 3.4 Percentage of quadrats with four cover categories as a function of distance from the base of a *Grevillea* shrub, summed for all census dates for each site.

No clear pattern of seasonal seedling dynamics emerged during the study period (Table 3.2). Low seedling numbers in bare patches in particular gave mixed results. There were no seasonal changes in mean seedling densities either under *Grevillea* canopies, or in bare gaps at Lake Augusta. Lake Botsford also recorded no change in seedling densities under *Grevillea* or in bare gaps between 100 and 150 cm from *Grevillea* base, but there were more seedlings in February 2002 at 75-100 cm and in April 2003 at 50-75 cm compared to August/September 2002. At Carter Lakes, there were more seedlings under *Grevillea* in February 2002 than in February/March 2001, more seedlings in bare quadrats at 50-75 cm compared to May - July and December 2002, and more seedlings in bare gaps between 75-150 cm than for all other census dates. Those higher summer and autumn seedling numbers in gaps at both sites were clearly not sustained through winter and spring. At Liawenee Moor Exclosures,

February, April/May and December 2002 censuses recorded more seedlings under *Grevillea* than in February 2001. However, there were no changes in bare gaps between dates.

Table 3.2 Results of analysis of variance of the effect of census date on seedling densities within each transect section at each site. NS, non-significant; -, analysis not possible.

	0-25cm	25-50cm	50-75cm	75-100cm	100-125cm	125-150cm
Lake Botsford	*NS* $F_{3,159}=2.70$	*P=0.004* $F_{3,159}=4.66$	*P=0.012* $F_{3,159}=3\ 77$	*P=0.032* $F_{3,137}=3.03$	*NS* $F_{3,71}=0.97$	*NS* -
Carter Lakes	*P=0.003* $F_{4,124}=4.16$	*P=0.008* $F_{4,124}=3.61$	*P=0.023* $F_{4,114}=2.96$	*P=0.002* $F_{4,102}=4.64$	*P=0.003* $F_{4,68}=4.51$	*P=0.022* $F_{4,45}=3.18$
Exclosures	*P<0.0001* $F_{3,104}=10.35$	*P=0.001* $F_{3,104}=5.78$	*NS* $F_{3,98}=2.59$	*NS* $F_{3,81}=1.42$	*NS* $F_{3,58}=2.58$	*NS* $F_{3,41}=1.75$
Lake Augusta	*NS* $F_{4,40}=1.86$	*NS* $F_{4,40}=0.73$	*NS* $F_{4,39}=1.09$	*NS* $F_{4,37}=1.65$	*NS* $F_{4,22}=1.23$	-

In February and December 2002, more seedlings were recorded at the Liawenee Exclosures and Carter Lakes than at Lake Augusta or Lake Botsford, both under *Grevillea* and in some bare patches (Table 3.3). In April 2003 on the other hand, when no census was conducted at Liawenee Exclosures, only seedling numbers under *Grevillea* were higher at Carter Lakes than at Lake Augusta and Lake Botsford, with no differences between the three sites in bare gaps.

Table 3.3 Results of analysis of variance of the effect of site on seedling densities within each transect section for selected census periods. NS, non-significant; -, analysis not possible.

	0-25cm	25-50cm	50-75cm	75-100cm	100-125cm	125-150cm
February 2002	*P<0.0001* $F_{3,97}=11.63$	*P=0.0003* $F_{3,97}=6.83$	*P=0.0008* $F_{3,94}=6.11$	*P=0.008* $F_{3,80}=4.18$	*P=0.019* $F_{3,49}=3.65$	*NS* $F_{2,25}=2.45$
December 2002	*P<0.0001* $F_{3,98}=12.15$	*P=0.0003* $F_{3,98}=6\ 99$	*P<0.0001* $F_{3,94}=8.55$	*P=0.0004* $F_{3,84}=6.80$	*NS* $F_{3,48}=2.56$	*NS* $F_{2,27}=2.36$
April 2003	*P<0.0001* $F_{2,70}=19.41$	*P<0.0001* $F_{2,70}=10.56$	*NS* $F_{2,69}=0.89$	*NS* $F_{2,61}=1.78$	*NS* $F_{2,34}=0.33$	*NS* -

The majority of seedlings recorded were at a very early stage of development, and could only be identified to class level, as monocotyledons or dicotyledons (Table 3.4). The majority of unidentified dicots were most likely members of the Asteraceae, while grasses probably comprised the bulk of unidentified monocotyledons. Seedlings of dominant shrubs were easily identified by their robustness and characteristic set of first leaves if present. Seedlings of Leucopogon species were also common at the two sites with the least developed grassy/herbaceous strata, Lake Augusta, and Carter Lakes (37.1 and 26.9 % of seedling counts).

In general, very few adults were present in the transects on the Central Plateau, but those that were encountered in the transects, did seem to be associated with *Grevillea* cover. All individuals/monocot clumps recorded at Lake Augusta were found in the 0-25 cm section of the transects, as were all the records at Carter Lakes. No adult plants were observed in transect sections more than 25 cm from the base of Grevillea.

Table 3.4 List of censused seedling taxa at each site. Values are percentages of all seedlings counted for all sample periods.

Lake Botsford	%	Carter Lakes	%	Lake Augusta	%	Exclosures	%
Unidentified monocots	37.7	Unidentified dicots	27.0	*Leucopogon* sp.	37.1	Unidentified dicots	41.2
Unidentified dicots	28.3	*Leucopogon sp.*	26.9	Unidentified dicots	29.3	Unidentified monocots	24.0
Grevillea australis	11.6	Unidentified monocots	15.8	*Acaena sp.*	12.2	*Viola betonicifolia*	13.1
Orites sp.	7.4	*Acaena sp.*	7.6	Unidentified monocots	11.0	*Asperula gunnii*	9.7
Luzula sp.	5.7	*Grevillea australis*	7.5	*Oreomyrrhis sp.*	6.3	*Cerastium glomeratum*	4.9
Acaena sp.	2.9	*Orites sp.*	4.8	*Orites sp.*	1.5	*Luzula sp.*	4.0
Asperula gunnii	2.7	*Luzula sp.*	3.0	*Luzula sp.*	1.2	*Oreomyrrhis sp.*	1.1
Oreomyrrhis sp.	2.2	*Viola sp.*	2.7	Unidentified graminoids	0.5	*Grevillea australis*	0.7
Viola sp.	0.8	*Asperula gunnii*	2.4	*Grevillea australis*	0.5	*Leucopogon sp.*	0.5
Hydrocotyle sp.	0.3	*Oreomyrrhis sp.*	1.3	*Cardamine sp.*	0.2	*Epacris sp.*	0.4
Cerastium sp.	0.2	Unidentified graminoids	0.5	*Viola sp.*	0.2	*Ranunculus sp.*	0.2
Geranium sessiliflorum	0.1	*Geranium sessiliflorum*	0.2			*Acaena sp.*	0.1

Senecio sp.	0 1	*Hydrocotyle sp.*	0 2	*Taraxacum officiniale*	0.04
		Cardamine sp.	0.2	*Geranium sessiliflorum*	0.04
		Rununculus sp.	0 04		

DISCUSSION

Facilitation of plant establishment by nurse species has been observed in a wide range of stressful environments, including alpine systems (Kikvidze & Nakhutsrishvili 1998; Nuñez *et al.* 1999; Arroyo *et al.* 2003; Olofsson 2004; Cavieres *et al.* 2006). Similarly, this study illustrates the positive effect of *Grevillea australis* canopies on seedling density in alpine vegetation on the Central Plateau. The pattern of higher seedling numbers under the nurse shrub compared to open microhabitats was consistent across sites and seasons, and therefore *Grevillea* is likely to play a vital role in facilitating many species. However, is this pattern attributable solely to *Grevillea* providing a safe site for seedling emergence or survival, or does greater seed interception and accumulation by the shrub also paly a role? (cf. Bullock & Clarke 2000; Bullock & Moy 2004). This question of uneven seed dispersal is addressed in Chapter 4, while Chapter 5 considers post dispersal seed removal by invertebrates.

Regardless of any other factors involved, the microhabitat under *Grevillea* canopies clearly provided a "safe site" for germination and survival resulting in seedling presence, while adjacent bare areas were consistently less favourable, although prolific germination was observed in bare patches at Liawenee Exclosures (Figure 3.5). Drier communities like grasslands and arid systems do not appear to need gaps or disturbance for emergence like more mesic environments, as protection from desiccation (and often high radiation and temperature), afforded by the proximity to other vegetation is more important (Fowler 1986; Fowler 1988; Castro *et al.* 2004). Welling and Laine (2002)

found there was no difference in seedling numbers in gaps and closed vegetation in sub-arctic heath and meadow communities where drought in gaps reduces emergence. Likewise, intertussock gaps did not provide recruitment sites for native forbs in Australian grasslands (Morgan 2001; Clarke & Davidson 2004). In limestone grasslands of northern Switzerland, existing vegetation increased seedling survival of some species by up to 10 times compared to bare patches, by limiting or preventing drought and frost heave (Ryser 1993). Cooper *et al.* (2004) reported that seedling density was higher in intact than in disturbed (roadside and mining installation) *Dryas* heath in the high Arctic (Svalbard), where recruitment was limited by availability of safe sites in disturbed heath.

In contrast, Williams (1992) found that shrubs did not establish in gaps less than 25 cm diameter in subalpine grassland and open heath of the Bogong High Plains, possibly due to competition from surrounding tussocks. In this study however, facilitation by the established shrubs appears to outweigh any detrimental effects from competition as even the dominant shrub seedlings *Grevillea australis* and *Orites spp.* were found predominantly under *Grevillea* canopies at all sites, with very few, if any, seedlings of these species in bare gaps. Although this could be explained by the large size of *Grevillea* seeds, which are unlikely to travel very far from the parent plant, *Orites spp.*, which could be some distance away, must have dispersed to this microhabitat. Establishing in bare ground limits competition, but in mountain environments, even shrub seedlings become more prone to frost heave in open areas if low temperatures and high soil moisture conditions coincide, while also being subject to desiccation in periods of high temperatures and low rainfall. It is also worth noting that the size of gaps examined in this study was at least four times those described by Williams (1992), with most gaps at least a metre in diameter.

Figure 3.5 Flush of dicot seedlings in a gap at Liawenee Exclosures, April 2003.

The microtopographic features of gaps could also be important. Large rocks, or features such as coarse substrate or concave surfaces which trap seeds and moisture can enhance recruitment of pioneer species during primary succession (Jumpponen *et al.* 1999). Coarse substrates may also limit mechanical disturbance due to frost heave compared to finer material. Erschbamer and co-workers (2001) found most seedlings on a glacier foreland emerged in safe sites in the vicinity of already established plants and larger stones rather than in bare ground where conditions were too dry for germination. No significant differences in seedling numbers were observed between bare soil quadrats in this study, suggesting microtopographic factors were less critical for seedling recruitment at the microhabitat level than *Grevillea* cover. Their potential influence at the finer, seedling microsite scale of centimetres or even millimetres however, cannot be overlooked.

Shrubs and cushion plants (in alpine communities) appear to be most effective facilitators for a variety of seedling species, mainly due to the protection from drought

they afford. Moles and Westoby (2004) concluded that, based on the literature reviewed, drought, followed by herbivory and pathogen attack, are the major causes of seedling mortality with only a small proportion of deaths attributable to competition from other seedlings. Drought claimed most 1 year old seedlings of the saguaro giant cactus in the Sonoran Desert (Steenbergh & Lowe 1969), and was also a major cause of mortality for Arroyo willow seedlings in northern Arizona (Sacchi & Price 1992). In Mediterranean dense scrub in southern Spain, survival of *Olea europaea* seedlings was highest under two shrubs (but not conspecifics), whereas no seedlings survived in the open, with mortality largely caused by drought (Rey & Alcántara 2000). Castro et al. (2004) found that in drought prone Mediterranean habitat shrubs facilitated emergence and survival of *Pinus sylvestris* seedlings, with summer drought being the most important cause of mortality. The nurse shrubs reduced radiation and soil temperature, and increased soil moisture and air humidity, which in turn would improve water status of seedlings. This was evident in higher survival of seedlings on the northern side of the shrubs, which would support the effect of shading. Franco and Nobel (1989) present evidence that nurse plants facilitate the growth of cacti through reduced maximum soil surface temperature, while cushion plants in the Patagonian Andes are postulated to act through providing milder surface and soil midday temperatures, shelter from wind and greater water availability (Arroyo *et al.* 2003). Brittingham and Walker (2000) also speculate on the importance of moderated tissue temperature and alterations in light intensity and shade by the nurse plant as the most critical parameters in *Yucca brevifolia* seedling survival in a desert environment. These findings from arid and/or shrubby systems are also relevant to the structurally similar Central Plateau study sites, with relatively dry summers, eroded soil profiles, and patchy vegetation.

Shrubs may have complex effects on associated species, however, as reduced light levels can translate to reduced photosynthesis for plants under the canopy (Forseth *et al.* 2001), and root competition can negate any protective effects and result in poor seedling survival and growth (Aguiar *et al.* 1992). Franco and Nobel (1988) found that although the desert bunchgrass facilitates *Agave deserti* seedling establishment, shading decreases surface carbon dioxide uptake, which together with competition for water, reduce

seedling growth. Reduced growth due to lower radiation was also observed in *Pinus sylvestris* seedlings associated with shrubs (Castro *et al.* 2004), and shading was experimentally verified to decrease seedling size in *Salix lasiolepis* (Sacchi & Price 1992). Nevertheless, there is evidence that a reduction in irradiance can be beneficial to growth during periods of stress in frost-prone environments (Egerton *et al.* 2000). Even if competition from the *Grevillea* shrubs was exerting a negative effect on seedling growth, it is likely that growing in bare exposed patches was even more hazardous to a seedling's progress, as the conspicuous absence of adults in that microhabitat would suggest. However, because the establishment of at least some of the adult plants may have occurred prior to the expansion of the *Grevillea* canopy, and may have been facilitated by microtopographic features, the impact of canopy cover on long term survival is best examined by following individual seedlings.

There was no pronounced peak or fall in seedling numbers across all sites for any of the census dates, either under *Grevillea* or in gaps. Pulsed emergence and subsequent mortality of seedlings could have occurred but failed to be detected between successive counts several months apart (see Figure 3.5). It is most likely that any potential flush of seedlings would occur in response to rainfall events (see Chapter 5), which is why seedling numbers were relatively high in February 2002. Bureau of Meteorology data indicates that in the four weeks prior to the 13- 23 February 2002 seedling census Liawenee recorded between 52 to 62 mm of rainfall. This contrasts with approximately 22 mm of rainfall received in the four weeks prior to the 22 - 25 February 2001 count. Median rainfall for February and March at Liawenee is 39.4 and 42.4 mm respectively (see Table 1.1). Although facilitation was observed in stressful years, but not in wet years in some communities (Callaway & Walker 1997; Ibáñez & Schupp 2001), *Grevillea* was positively associated with seedlings even during the relatively wet period in February 2002. Without more frequent surveys and/or tracking of individuals however, it is uncertain whether this was due to greater germination or high seedling survival, or both. Fuentes and colleagues (1984) found that even in unusually wet years, all seedlings of several shrubs between existing clumps of shrubs in Chilean matorral vegetation, at the foothills of the Andes (c. 1000 m a.s.l.), desiccated in the dry season,

whereas a large proportion of seedlings under or around established clumps of shrubs survived.

Grevillea australis plays a crucial role in promoting recruitment and regeneration of many species on the Central Plateau. The facilitation is most likely due to protection from drought and frost heave and this effect will depend on time of emergence of individuals, and is likely to be important even during a relatively wet growing season. In addition, protection from herbivory and trampling (by wombats for example) or other stochastic events like hailstorms could also contribute to the pattern of seedling aggregation under *Grevillea* canopies. Seedling mortality caused by native and introduced herbivores could be a particularly interesting research area to explore, together with studies of long term seedling survival. The presence of large gaps is clearly limiting recruitment in these shrubby alpine communities and colonization of bare ground is unlikely to occur via seedling establishment in large, eroded patches, away from the protection of existing vegetation like *Grevillea australis*.

Chapter 4. Seed rain

INTRODUCTION

Understanding seed rain dynamics is essential to understanding recruitment and regeneration in plant communities, and thus the potential for change, particularly in those communities where vegetative expansion is uncommon. Recruitment of individuals depends on their successful establishment, which depends on seed production and dispersal into a suitable environment, or a "safe site" (Harper 1977). Seed dispersal has two phases: primary dispersal of seeds from the parent plant, and the secondary distribution into subsequent locations (Chambers & MacMahon 1994). Some microsites can trap or preferentially retain seeds, attract seed predators, or be particularly favourable to germination, hence the structural heterogeneity of the environment is an important determinant of seed dispersal and survival patterns (Fuentes *et al.* 1984; van Tooren 1988; Chambers *et al.* 1991; Aguiar & Sala 1997; Russell & Schupp 1998). However, the role of microhabitat is often unexplored in seed dispersal studies (Russell & Schupp 1998; Nathan & Muller-Landau 2000), and many models which assume a smooth decline in seed density with distance from the parent are likely to be oversimplifications (Bullock & Clarke 2000), especially in heterogenous systems like deserts or shrubby vegetation (Bullock & Moy 2004).

Seed deposition is also an essential first step in colonisation of disturbed areas which might be lacking a source of colonists in the seed bank due to degraded soil structure and limited vegetation cover. Although seed arrival is no guarantee of recruitment, recruitment cannot occur without seed arrival. Understanding the spatial and temporal patterns of propagule deposition is therefore particularly relevant to the assessment of self-recovery or restoration efforts (Urbanska *et al.* 1999).

Community level seed rain studies are relatively rare in the literature, although there have been several published studies from alpine and tundra regions in the last 15 years (Table 4.1). Targeting single species is more practical when examining predation, gene flow or invasibility potential of populations rather than general community dynamics, and numerous such species-specific seed dispersal studies exist. Single populations have also been focused on more often because of the difficulties with designing trapping methodology that samples all seed types with equal reliability and success in a community. This problem is reduced in herbaceous or low stature vegetation like grasslands or heathlands, where propagule size and release height are relatively uniform, making such communities less challenging to study in this respect than forest systems (Rabinowitz & Rapp 1980).

This study was undertaken to assess seed availability in three alpine communities on the Central Plateau and the possible role of seed rain in limiting recruitment and regeneration of degraded areas. In particular, the questions addressed were:

1) How does seed abundance vary seasonally in the landscape?
2) What is the pattern of seed deposition in different microhabitats?
    a) Do open, bare patches receive less seed fall than other microhabitat types?
    b) Do they receive fewer species or distinct suites of species?

Table 4.1 Comparative estimates of total seed rain in alpine vegetation from the literature

Source	Site	Community/Veg type	Time	Trap design	Number of species	Seeds m^{-2}
This Study	Central Plateau, c.1000masl, Tasmania	Grassy shrubland Shrubby alpine heath	March 2002 – April 2003	Dry plastic funnels, 6.5 cm diameter	19 13 - 24	10 113 7 520 - 10 506
Spence 1990	Craigieburn Valley, c.1500masl, New Zealand	Herbfield Snowbank Grassland	January to May	Dry 8.5 cm diameter pitfall traps	11 - 12 9 - 13 4 - 9	741 - 1 164 3 809 - 8 871 1 623 - 2 275
Marchand and Roach 1980	Franconia Ridge, c.1525masl, White Mountains, New Hampshire	Dwarf shrub heath-rush community	August to October	13x13 cm plexiglass plates covered with sticky, non-drying material	4	2 538
Chambers (1993)	Bearthooth Plateau, Montana, 3200masl	Late seral Geum turf vegetation Disturbed borrow area	mid July to mid September	Dry plastic funnels, 10 cm diameter	24 - 54 16 - 36	3 375 - 6 179 7 730 - 14 009
Stöcklin and Bäumler (1996)	subalpine belt of the Central Alps	Glacier forleland	July to October	Water filled trays	11 - 19	125 - 2 333
Erschbamer *et al.* 2001	Central Alps, 2400masl	Glacier forleland	July to October	Dry plastic funnels, 10 cm dimeter	7 - 23	3 809 - 6 598*
Urbanska and Fattorini (2000)	Jakobshorn Mountain, 2450masl, Switzerland	restoration plots at an alpine ski run	spring snowmelt until late autumn	Dry plastic funnel traps, 11.5 cm diameter	6 - 13	1 096 - 3 557
Urbanska *et al.* 1998	Jakobshorn Mountain, 2500masl, northeast Swiss Alps	grassland	July to September	Dry plastic funnel traps, 11.5 cm diameter	15	471 - 1 673
Ryvarden 1971	Finse, c.1500masl, South Norway	Base of retreating glacier	July to beginning of September	Water filled trays, 60 x 40 cm	-	342 – 653
Molau and Larsson 2000	Latnjajaure, northernmost Swedish Lapland tundra, 380 – 1560masl	birch forest, sparsely forested heath, shrubby meadow, low scrub heath, poor heath, alpine meadow	late summer, autumn and winter	0.25m^2 plastic FinTurf doormats	8 - 48	11 - 1 362
(Welling & Laine 2002)	Kilpisjärvi, sub-arctic Finland (69°01'N), low alpine zone, 650-720m a.s.l.	Heath Meadow	Early August 1997 to early July 1998	Green, plastic turf mats	?	c. 300 c. 1000

*calculated from numbers of seeds per trap

METHODS

Seed rain was monitored at the sites using dry funnel traps. Trap design was based on that proposed by Schott (1995) for monitoring seed rain in grassland communities. A trap consisted of a 65 mm diameter flexible plastic PE funnel, inserted inside a 65 mm wide (internal diameter) and 80 mm long PVC pipe sunk into the ground (Figure 4.1). This gave a trapping area of 33.18cm^2 per unit. The relatively small trap size was needed to accommodate the rocky substrate at some sites, which made digging and insertion of the traps into the ground difficult. Small seed traps are also preferable in grasslands or herbaceous vegetation to cope with the small scale heterogeneity of these communities (Willems & Bik 1998). The funnel was about 45 mm deep, cut off just above the stem to give an aperture of c. 20 mm diameter. Fine nylon/polyester fabric was folded and sewn together to form a square pocket, which was held in place between the PVC pipe and the funnel (Figure 4.1). To change the seed trap, the funnel was pushed into the PVC pipe and removed with the nylon pocket containing seeds. A new bag was placed inside the PVC pipe and secured at the top by re-inserting the funnel. The top of the bag was folded over the top of the pipe and held in place by a rubber band. About 1 cm of the pipe protruded aboveground to prevent soil and invertebrates from entering the trap. This was not enough of a deterrent however, and numerous invertebrates had become trapped in the nylon bag. Traps in open bare areas also accumulated some soil due to wind deposition. Animal disturbance was a problem at some sites, so 1cm^2 wire mesh guards were placed over the traps.

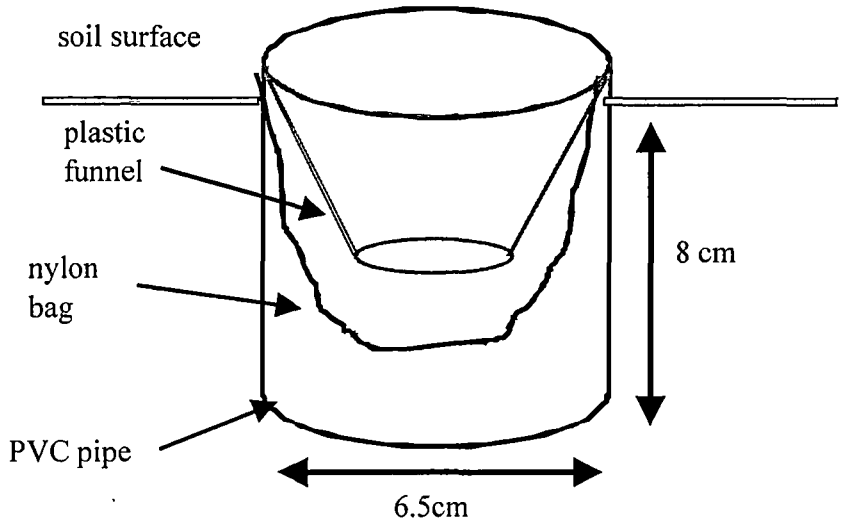


Figure 4.1 Funnel seed trap in cross section.

Similar trap designs have been previously used successfully in alpine communities (Spence 1990; Urbanska *et al.* 1998; Urbanska *et al.* 1999; Urbanska & Fattorini 2000) and elsewhere. This type of trap has also been shown to be advantageous in windy environments where a commonly used sticky surface design (Werner 1975; Huenneke & Graham 1987) would dry out quickly and accumulate dust, invertebrates and debris, thus making seed retrieval more time-consuming and less successful (Kollmann & Goetze 1998). Sticky traps are also less effective at capturing propagules without awns or hairs (Huenneke & Graham 1987). The funnel trap is less likely to resuspend seeds due to flooding or wind, or lose seeds to predators like birds and rodents (Johnson & West 1988), and is particularly effective in measuring local seed production (Chabrerie & Alard 2005). Funnel traps have been found to be most efficient, catching the most seeds as well as species compared to other types of traps (Page *et al.* 2002; Chabrerie & Alard 2005).

The traps were deployed in various microhabitats around prostrate *Grevillea* shrubs to assess the numbers of seeds and species arriving in bare areas (Bare), in vegetation patches (Control), at the edge of the *Grevillea* (Edge), and under the *Grevillea* branches (Grevillea) (Figure 4.2). Five *Grevillea* shrubs (replicates) per site were selected except at the Exclosures, where only four suitable shrubs could be found, but where two additional bare traps were set up independent of a *Grevillea*. One trap was placed in each microhabitat type (four per shrub), giving a total of 20 traps per site, except at the Exclosures, where a total of 18 traps were installed. The microhabitat patches ranged from approximately one to several meters in diameter, with the traps around a replicate shrub arranged within an area of 2 m radius. The seed traps were changed at monthly intervals (every 25 to 34 days) for 14 months, therefore sampling two major periods of seed dispersal and, in addition, assessing dispersal at other times of the year. In March 2002, due to logistical considerations the traps were collected after only 14 days at Carter Lakes, after 16 days at Lake Botsford, and after 21 days at the Exclosures. Collection in June 2002 was prevented by heavy snowfalls during the weeklong trip, so the July 2002 data is equivalent to two months' sampling. Although weekly or fortnightly sampling would have been desirable, the remote location of the site made this impractical. Any live invertebrates trapped in the bags were removed, but many dead specimens were left intact for later identification. Immediately after collection, the nylon/polyester bags containing seeds were dried at room temperature and stored on a lab bench until processing. The content of the bags was weighed, and the seeds were counted and identified using a dissecting microscope. Only healthy, filled seeds were counted. Seed identification was aided by field collections, but members of the *Poaceae* and *Asteraceae* could not be satisfactorily identified to genus or species level, and between 21% (Exclosures) and 29% (Carter Lakes) of seeds remained unidentified. Therefore, the term 'taxa' is used here instead of species to include these higher taxonomic groupings.

Figure 4.2 Funnel seed traps *in situ*, Edge location top right, and Bare location lower right.

In addition, the standing vegetation within a 10 m radius of the seed traps was also recorded at Carter Lakes and Lake Botsford, using seven randomly placed 3x3m quadrats. Only the nearby vegetation was sampled, as many studies have shown the short distance travelled by most seeds from parent plants was under 50cm (Spence 1990; Scherff *et al.* 1994; Stöcklin & Bäumler 1996).

Data analysis

The data was analysed with a mixed model ANOVA using general linear model (GLM) procedures in SAS ver.9.1 (SAS Institute Inc. 2002). To investigate the pattern of seed deposition in different microhabitats, total seed rain over the study period was analysed by a 2-factor ANOVA with site and microhabitat type as the two fixed factors, with

individual traps as replicates. A 2-factor repeated measures ANOVA using GLM procedures was performed when comparing seed densities and number of taxa across months to assess seasonal variation in seed rain abundance. Given that there was a significant time x site interaction ($P<0.0001$), data was analysed separately by site. Differences between samples were compared *post hoc* using the Ryan-Einot-Gabriel-Welsch Multiple Range Test (Day & Quinn 1989).

Bray-Curtis cluster analysis with group averaging was used in Biodiversity Pro (McAleece 1997) to explore similarities in seed rain composition between microhabitats.

RESULTS

Timing of dispersal and overall seedfall

Total seed rain density did not differ significantly between sites ($F_{2,46}=0.65$, $P=0.53$), with a total of 7 520 seeds m^{-2} recorded at Carter Lakes, 10 113 m^{-2} at the Exclosures, and 10 506 m^{-2} at Lake Botsford over 14 months (data based on cumulative seed rain). Overall, 24 seed rain taxa were identified at Carter Lakes, 19 at Liawenee Exclosures, and 13 taxa were found in the Lake Botsford traps during 14 months of sampling (Figure 4.3). In comparison, 31 angiosperm species were recorded in the adjacent standing vegetation at Carter Lakes and 36 at Lake Botsford (Figure 4.3). Although some seeds were not identified to species level, they were nevertheless split into morphologically distinct groups, and therefore it is unlikely that the seed rain component has been underestimated as a proportion of standing vegetation.

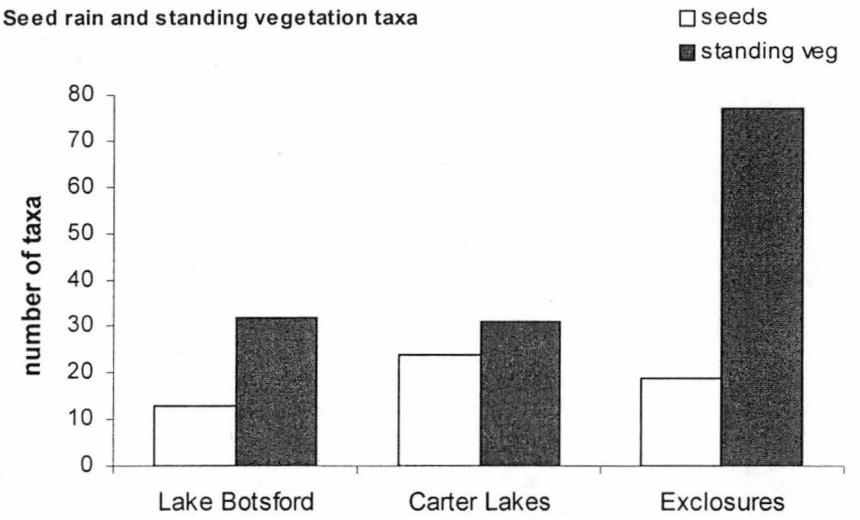


Figure 4.3 Total seed rain (pooled from all traps) and standing vegetation taxa (angiosperms only). Liawenee Exclosures standing vegetation data from Bridle & Kirkpatrick (1999).

The repeated measures ANOVA for seed rain density showed the site by sampling time interaction to be significant ($F_{24,715}$=3.55, P<0.0001), indicating periods of very high seed fall were not synchronous between sites (Figure 4.4). At Lake Botsford, the peak mean seed rain density occurred in March 2002 with 3 090 ±989.5 seeds m^{-2}. It was significantly higher than the average seed rain in the remaining months of that year, and in January and April 2003, but not significantly different from the means in February and March 2003 ($F_{12,247}$=4.03, P<0.001) (Figure 4.4a). At Carter Lakes, only April 2002 had significantly higher seed fall than all other sampling times ($F_{12,247}$=3.67, P<0.0001), with a mean of 2 806.7 ±1 140.6 seeds m^{-2} trapped that month (Figure 4.4b). The highest seed rain at Liawenee Exclosures was in January 2003, with an average of 2 779.5 ±1208.4 seeds m^{-2} recorded that month. It was significantly higher than all other sampling times except March 2002 and February 2003 ($F_{12,221}$=4.74, P<0.0001) (Figure 4.4c).

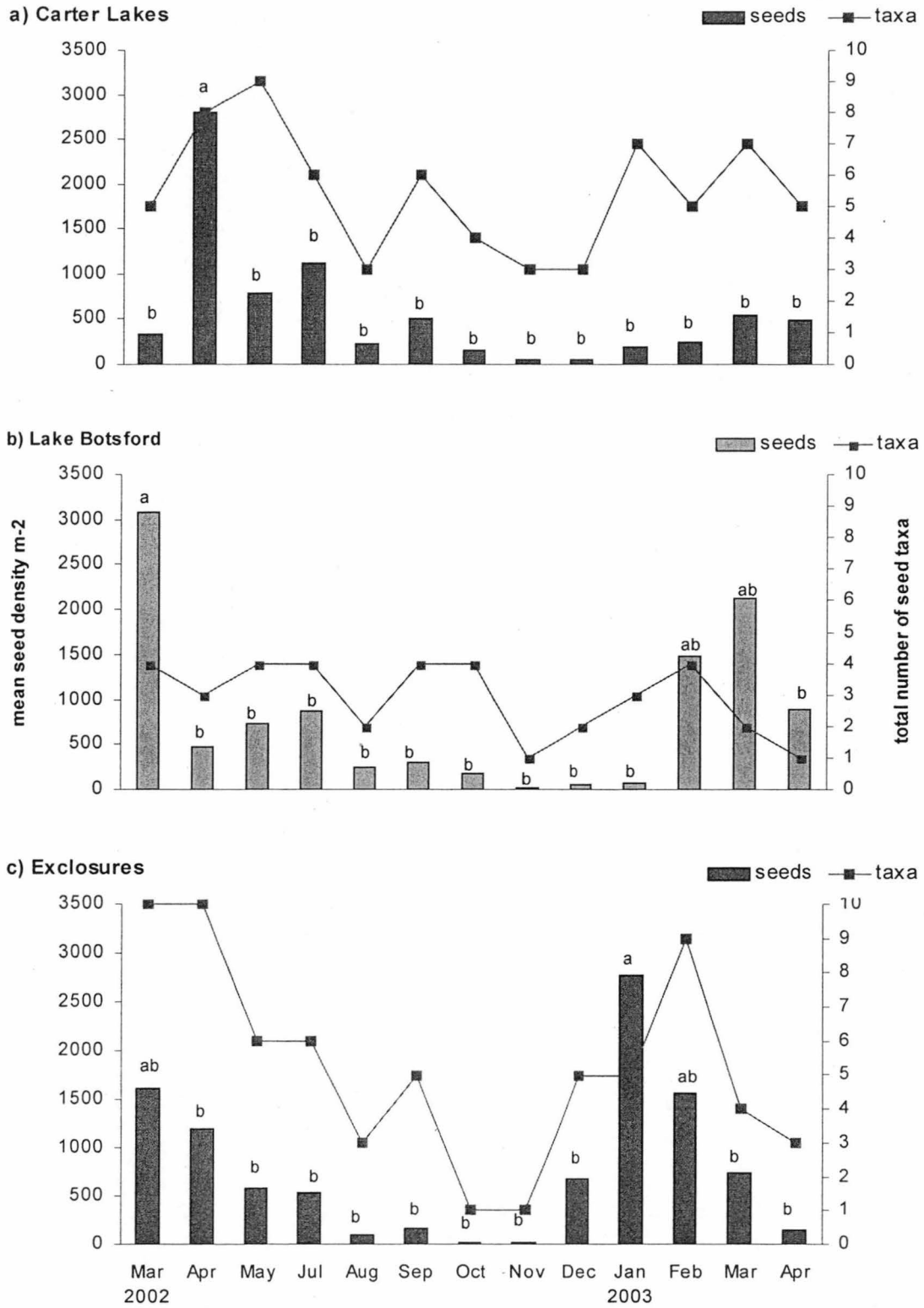


Figure 4.4 Seasonal changes in mean seed density m^{-2} and number of taxa at each site. Different letters indicate significant differences between months at P=0.05.

Species richness

The number of taxa captured in a given sampling session at a site varied between 1 and 10 (Figure 4.4). The lowest average number of taxa per trap at a site was recorded between October and December, but there was no clear seasonal pattern of species abundance, with a significant site by sampling time interaction ($F_{24,715}$=7.31, P<0.0001). At Lake Botsford, traps collected in July 2002 caught on average 1.25 ±0.23 taxa, which was significantly higher than the monthly samples for the rest of that year and for January and April 2003 ($F_{12,247}$=5.94, P<0.0001), but were not significantly different to the average numbers captured in March, April and May 2002, or February and March 2003 (Figure 4.5a). At Carter Lakes, traps collected in April 2002 had the highest average number of taxa (1.45 ±0.17), significantly above those collected in March, August through to December of that year, and January, February and April 2003 ($F_{12,247}$=4.73, P<0.0001), but were not significantly different to March 2003 samples, or those from May, July and September 2002 (Figure 4.5b). At the Exclosures, traps collected in March 2002 and February 2003 had significantly higher number of taxa on average (2.56 ±0.27 and 2.39 ±0.3 respectively) than those in all other sampling periods except April 2002 ($F_{12,221}$=15.5, P<0.0001) (Figure 4.5c). Average number of taxa per trap, or total number of taxa in a given month was not correlated with average seed density per month (r^2 = 0.4210 and 0.2071 respectively).

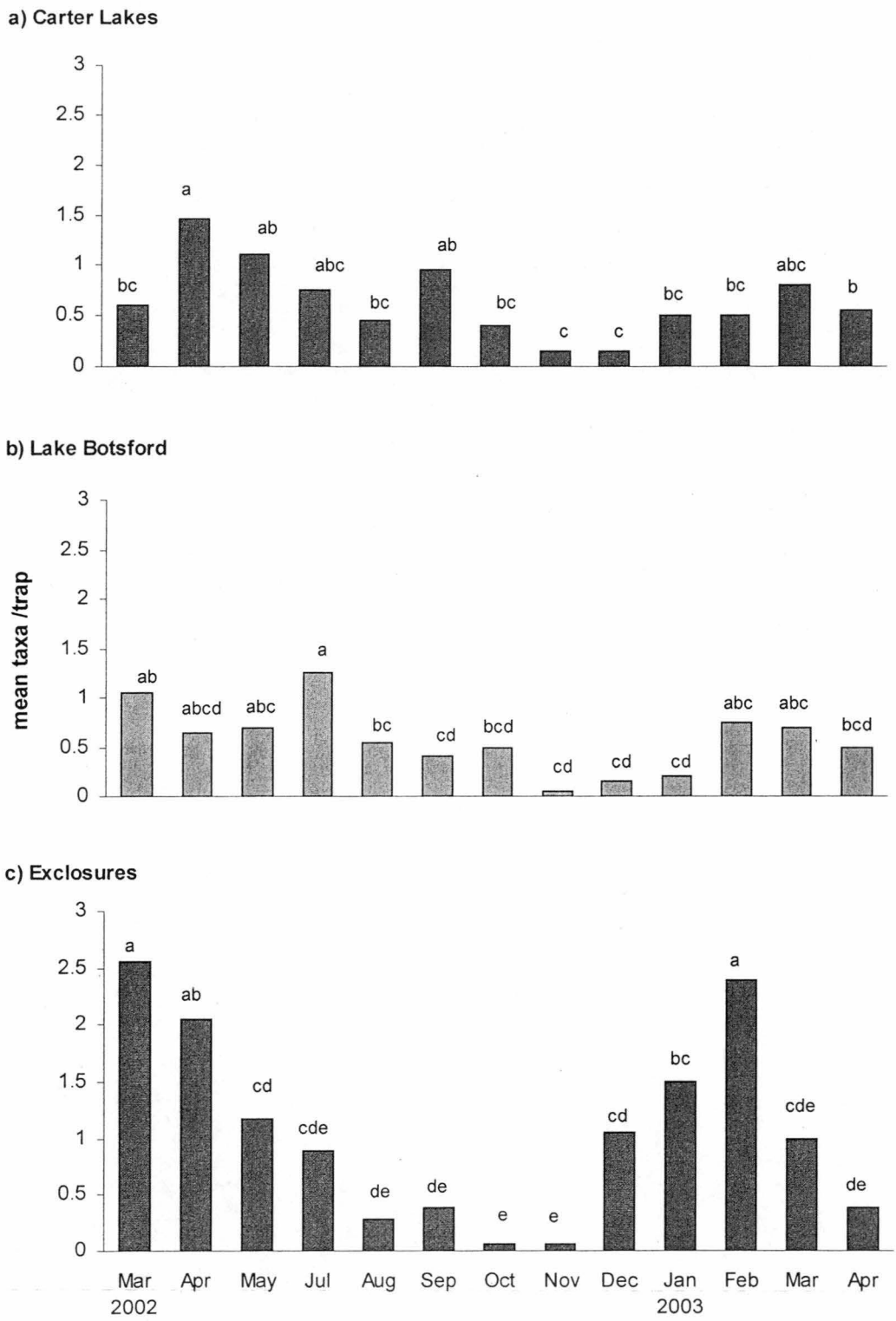


Figure 4.5 Seasonal changes in mean taxa per trap at each site. Different letters indicate significant differences between months at P=0.05.

Seed rain composition

Only one or two taxa dominated the seed rain at each site, with most taxa contributing less than 5% to total seed numbers. Small seeded species, such as *Epacris gunnii* made up 89.4% of the seed rain at Lake Botsford, and 36.8% at Carter Lakes. *Cerastium sp.* was the most abundant species at the Exclosures with 45.7%. The only other species to contribute more than 10% to the seed rain per site were *Ozothamnus hookeri* (28.8%) and *Orites acicularis* (11.3%) at Carter Lakes, and at the Exclosures, Asteraceae spp. 5 (15.1%) and 1 (10.6%), and *Agrostis* sp. (10.1%) (Figure 4.6).

The majority of species found in the Lake Botsford and Carter Lakes samples were shrubs, (50% and 35.3% of identified species respectively – unidentified species could have been shrubs), while the taxa sampled in the Exclosures were dominated by grasses (36.8% of all species – unidentified species did not include grasses) (Figure 4.7).

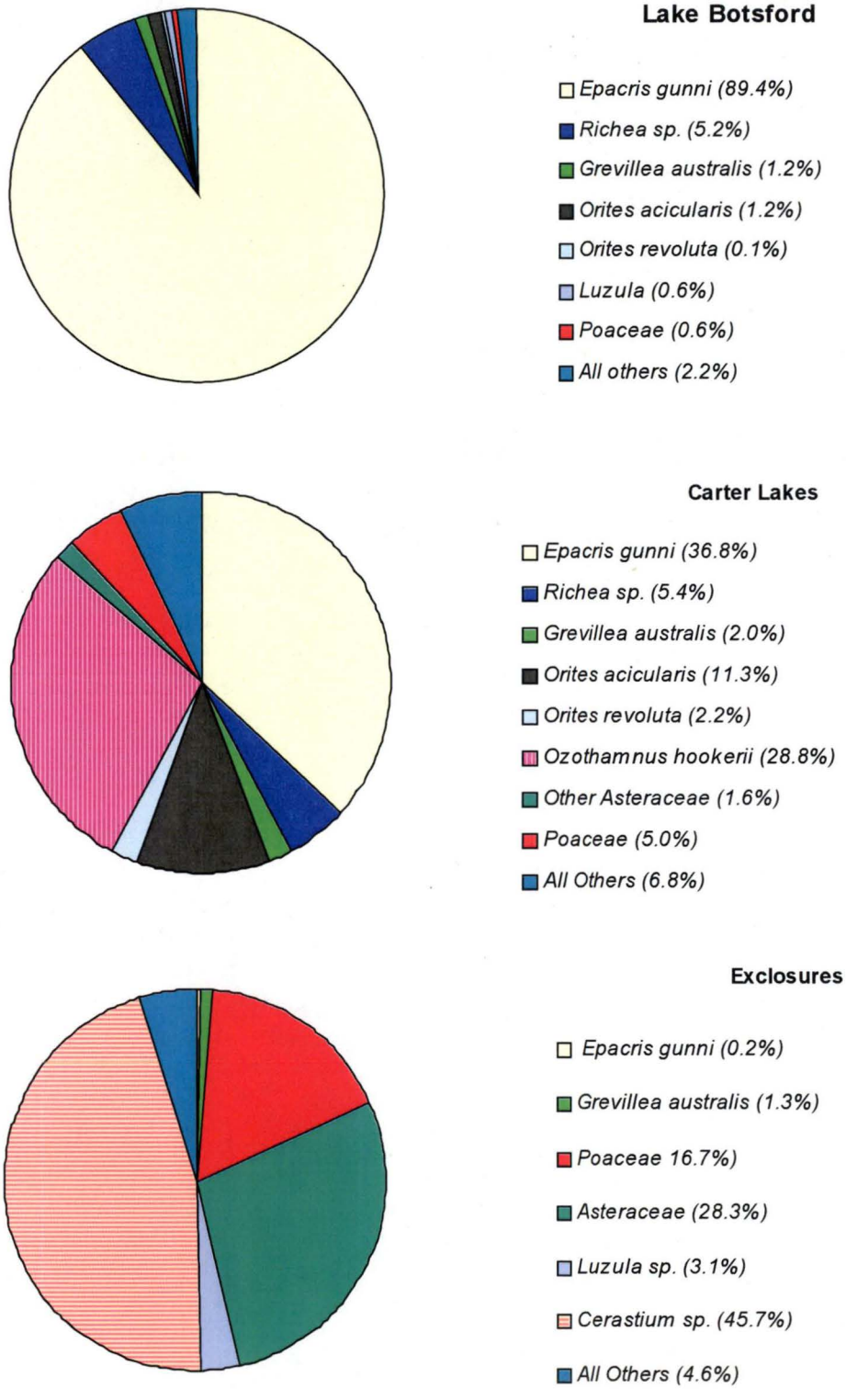


Figure 4.6 Seed rain composition at each site.

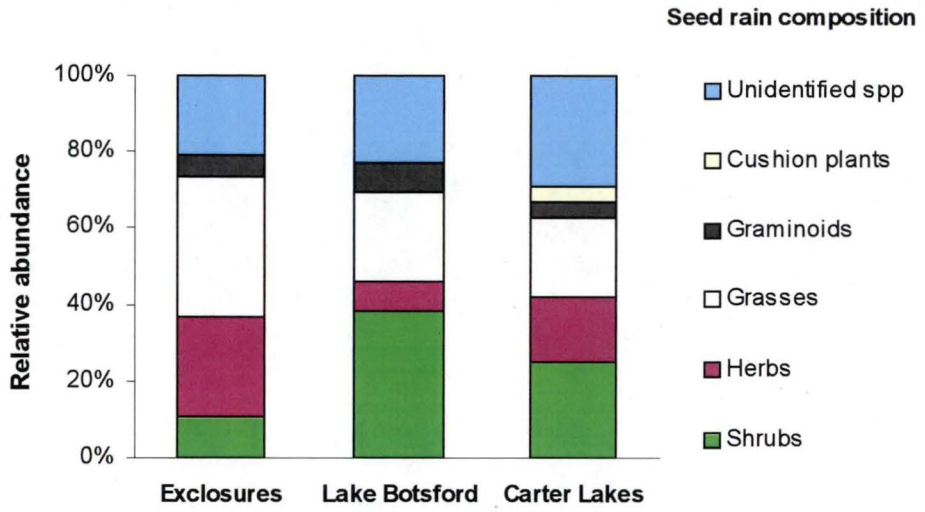


Figure 4.7 Functional group seed rain composition at each site. Herbs group excludes grass and graminoid seeds.

Seed deposition patterns in different microhabitats

There was a significant microhabitat effect on the total number of seeds trapped ($F_{3,46}$=3.47, P=0.02). Control traps captured significantly more seeds in the 14-month sampling period (mean 47.1 ±9.3 seeds) than traps under *Grevillea* (mean 15.4 ±3.4 seeds) (Figure 4.8). There was no site by microhabitat interaction ($F_{6,46}$=0.43, P=0.86), suggesting that the relative density of seed arrival among microhabitats did not differ between sites. There was no significant sampling time by microhabitat interaction either ($F_{36,552}$=0.93, P=0.60) (Figure 4.9). Microhabitat had a significant effect on *Grevillea australis* seed capture ($F_{3,54}$=8.54, P<0.0001), with the Edge traps capturing significantly more seeds than the remaining microhabitats (Figure 4.10).

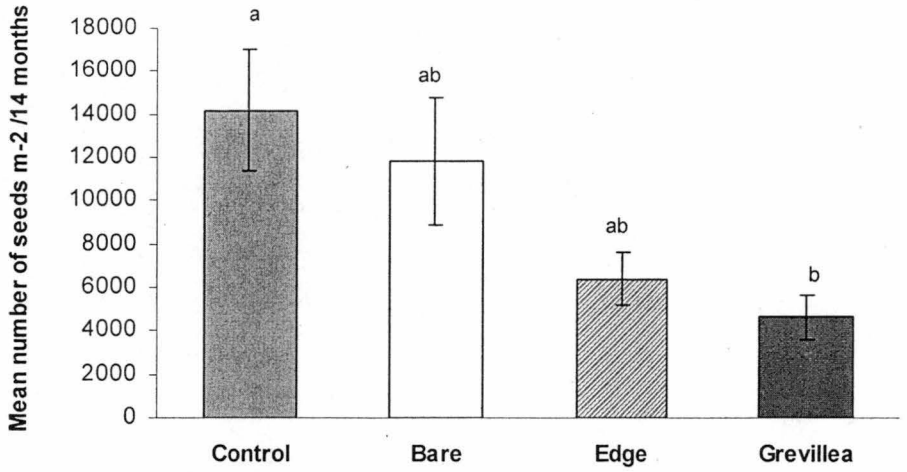


Figure 4.8 Effect of trap location on seed numbers captured. Different letters show significant differences between treatments at P=0.05. Bars are ± 1SE.

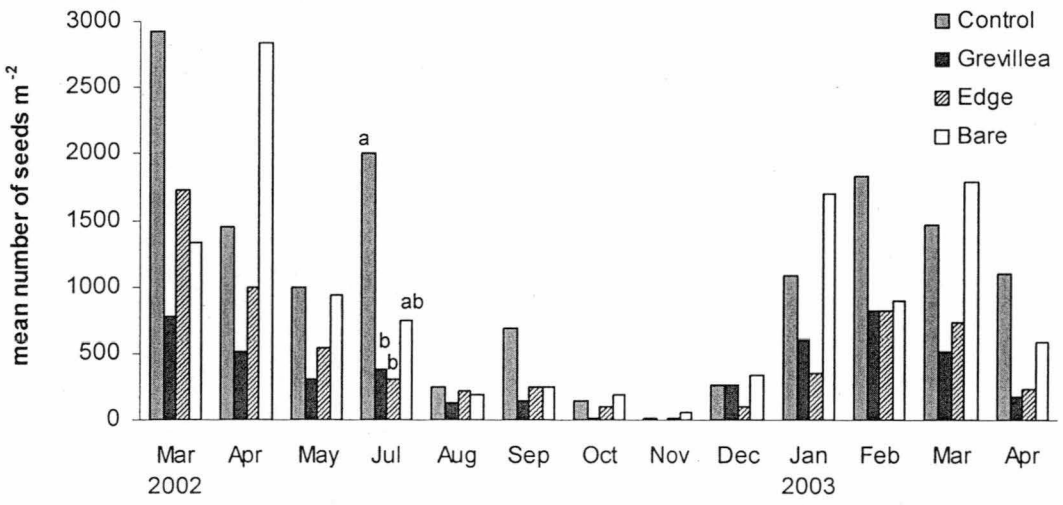


Figure 4.9 The effect of trap location on mean monthly seed density m^{-2} at all sites. Different letters show significant differences between treatments at P=0.05.

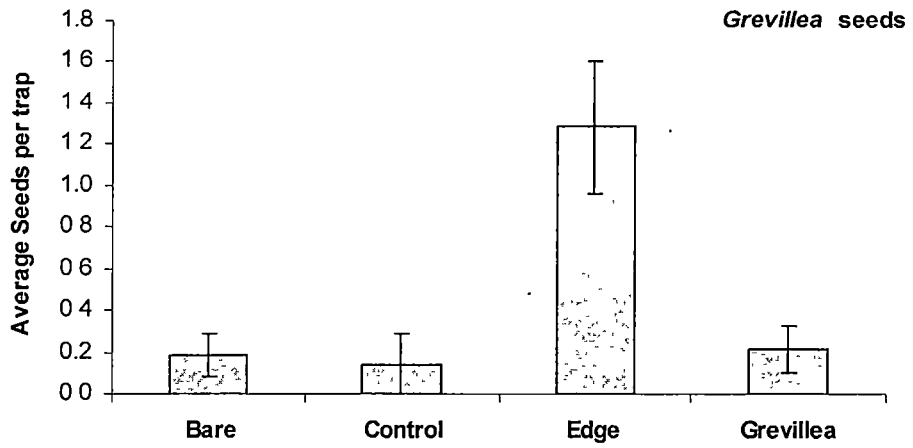


Figure 4.10 Microhabitat effect on entrapment of *Grevillea australis* seeds. Bars are ± 1SE.

Unlike seed rain density, the total number of taxa trapped during the 14-month sampling period did not differ between microhabitats ($F_{3,46}$=1.38, P=0.26). There was no site by microhabitat interaction either ($F_{6,57}$=1.06, P=0.40). When sites were analysed separately, Lake Botsford showed some significant differences between trap locations ($F_{3,16}$=3.26, P=0.049), with *Grevillea* traps capturing less taxa overall (mean of 1.6 ±0.19), than either Edge or Control traps (both with an average of 3.2 ±0.58 and ±0.49 taxa respectively) (Figure 4.11). Microhabitat differences at Carter Lakes and Exclosures did not near significance ($F_{3,16}$=1.1, P=0.56 and $F_{3,14}$=0.71, P=0.38 respectively).

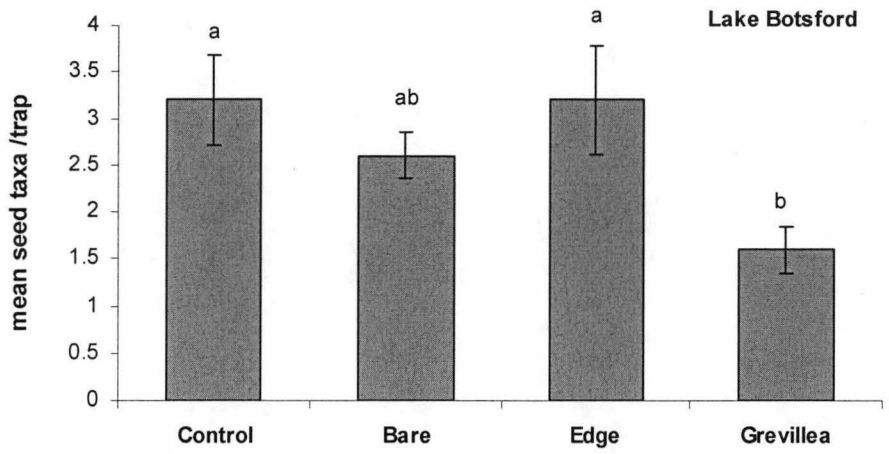


Figure 4.11 Lake Botsford – effect of trap location on total spp over 13 months. Different letters show significant differences between treatments at P=0.05. Bars are ± 1SE.

When the data was analysed on a monthly basis, there was a significant microhabitat effect ($F_{3,46}$=5.46, P=0.003) on the average number of taxa captured per trap, but once again no site by microhabitat interaction ($F_{6,46}$=1.01, P=0.43). Control traps have captured almost twice as many taxa as *Grevillea* traps in any given month, with a mean of 0.97 (±0.1) taxa per trap, compared to 0.55 (±0.09) taxa per trap per month (Figure 4.12).

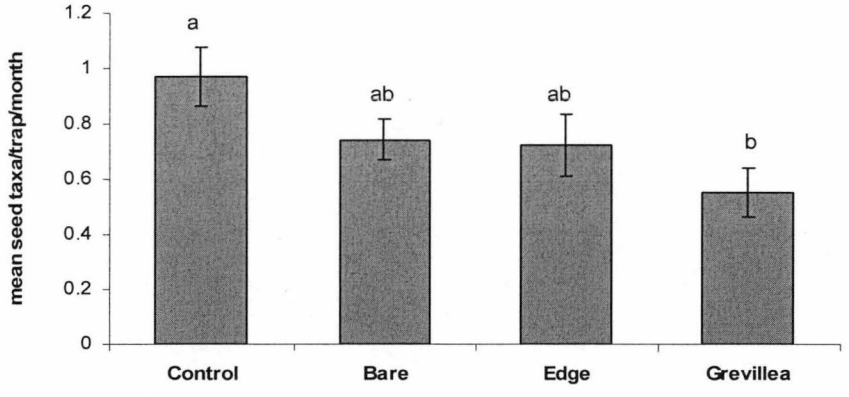


Figure 4.12 Average spp per trap per month. Different letters show significant differences between treatments at P=0.05. Bars are ± 1SE.

The repeated measures ANOVA for the number of taxa trapped showed that there was also a significant time by microhabitat interaction ($F_{36,552}$=1.63, P=0.01). Control traps in July 2002 trapped significantly more taxa (1.68 ±0.27 per trap), than *Grevillea* (0.57 ±0.14), or edge traps (0.55 ±0.2) (Figure 4.13). In March 2002 however, it was the edge traps that had significantly more taxa (mean 1.86 ±0.39), than the control (mean 1.14 ±0.29), or the *Grevillea* traps (mean 1 ±0.26 taxa). There were no significant differences in the number of taxa trapped based on trap location for the remaining 11 months.

The Bray Curtis Cluster Analysis for each site did not reveal any distinct suites of seed taxa based on microhabitat type. There were no groupings based around different *Grevillea* replicates either.

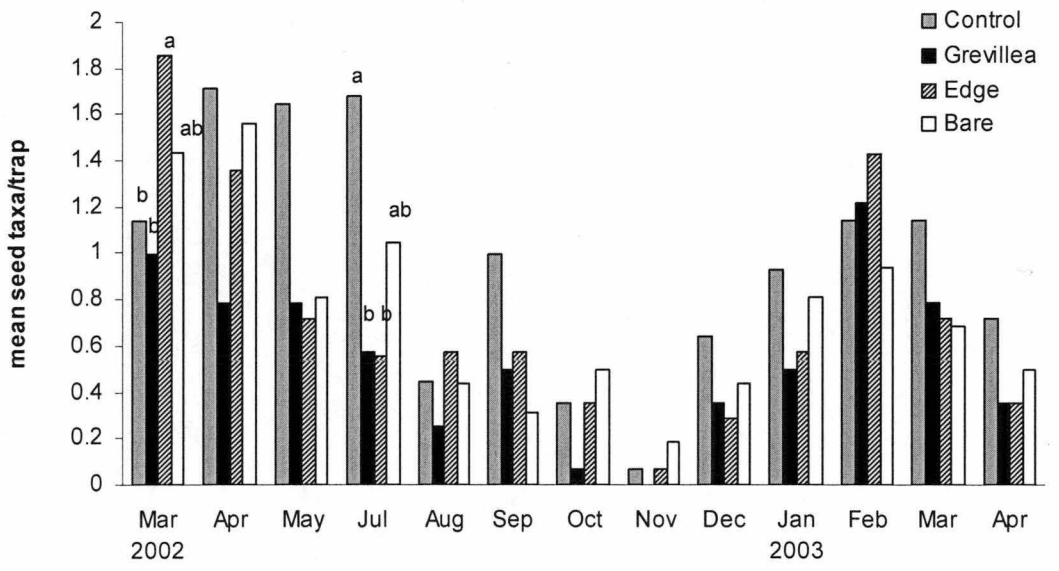


Figure 4.13 The effect of trap location on mean monthly species richness per trap at all sites. Different letters show significant differences between treatments at P=0.05.

DISCUSSION

The results of this study suggest that seed rain is not limiting revegetation of bare patches on the Central Plateau. Bare areas did not receive fewer seeds or taxa than other microhabitats. Seed rain density at all sites was comparable to, or higher than, that reported for other alpine regions. Table 4.1 summarises similar studies from Craigieburn Valley in New Zealand (Spence 1990); Bearthooth Plateau, Montana (Chambers 1993); glacier foreland in the Central Alps (Stöcklin & Bäumler 1996; Erschbamer *et al.* 2001) and Southern Norway (Ryvarden 1971); restoration plots at an alpine ski run (Urbanska & Fattorini 2000); an alpine grassland (Urbanska *et al.* 1998); and Swedish Lapland tundra (Molau & Larsson 2000). Seed densities from Mediterranean open shrubland and from transitional "steppic" vegetation with dwarf shrubs, and even desert systems in Israel are also comparable, with 3340, 7599 and, 3563 to 3806 seeds m^{-2} respectively reported (Holzapfel *et al.* 1993). In contrast, Rabinowitz and Rapp (1980) estimated the seed rain of a temperate tall grass prairie in Missouri at 19 726 seeds m^{-2} between June and December (26 weeks), while Schott and Hamburg (1997) recorded between 37 300 and 91 200 seeds m^{-2} from June to December in a native tall grass prairie in Kansas. There are no published reports of seed rain in alpine, grassland or shrubby vegetation from Australia.

Unlike other high altitude or latitude areas where seed rain has been investigated, conditions on the Central Plateau allowed sampling throughout winter to give a complete seasonal picture of seed dispersal. Although there was a general decline in seed numbers in late winter to early summer, there was no clear pattern of seed abundance that applied to all three sites. Seed dispersal was pulsed in summer and autumn, with low background levels of seeds throughout the year. The Liawenee Exclosures showed a peak in seed numbers in early summer, well ahead of Lake Botsford and Carter Lakes. This was due to higher number of grass and herbaceous species in the Exclosures dispersing earlier than the shrubby species dominant at the other two sites. The January peak at the Exclosures was attributed solely to large numbers of *Cerastium* sp. seeds. Liawenee Moor is situated 100 m lower than the other

two sites, which could also allow an earlier onset of the growing period and seed development. Similarly, the peak at Lake Botsford in March 2002 was due to a large number of *Epacris* seeds being dispersed at the time, and the April 2002 peak at Carter Lakes was a result of dispersing *Epacris gunnii* and *Ozothamnus hookeri* seeds. It should also be noted that the relatively high July values are equivalent to two months of data, as the traps were not collected in June due to deep snow lie. It is likely that some of the seeds retrieved from these traps were deposited in June, resulting in elevated July values.

Although this study has documented monthly variation in seed rain, many authors have reported large differences in seed numbers between years within a given landscape (Morris *et al.* 1986; Salonen 1987; Spence 1990; Chambers 1993; Kotanen 1996; Molau & Larsson 2000; Larsson & Molau 2001). This 14-month data set allows comparisons only between early autumn (March and April) 2002 and 2003. One of the difficulties with interpreting the March results is the differing length of time the traps were operational in 2002 and 2003. The shorter trapping periods during March 2002 (see Methods) probably resulted in fewer seeds captured that month. If the sampling periods were equal, it is likely that significantly more seed would have been caught in March 2002 than March 2003, especially at Lake Botsford and Liawenee Moor Exclosures, where March 2002 values were already higher than those for a longer sampling period in March 2003. The April values were significantly different only at Carter Lakes. This is possibly due to poor seed set in *O. hookeri* and *E. gunnii* in April 2003 compared to 2002, as they were the main contributors to seed rain in that period. In Arctic and alpine studies, differences in seed numbers between years have often been shown to correlate with climate data for the preceding season, when the seeds were formed and dispersed (Marchand & Roach 1980; Chambers 1993; Larsson & Molau 2001). On the Central Plateau, the spring and summer rainfall of the current season was most likely to influence seed numbers. According to Bureau of Meteorology data for that area of the state, October 2002 to February 2003 was drier than the same period in 2001/2002. Although March and April of 2003 were wetter than the same period in 2002, it would have been too late in the season to affect flower and seed development. Fewer species

were also caught in March and April 2003 than the same period in 2002, with the trend particularly pronounced at the Exclosures.

Seed densities among microhabitats were surprisingly similar in such a structurally heterogenous landscape. Bare microhabitats captured comparable numbers of seeds to those trapped in vegetated patches, at the edges of *Grevillea*, and directly underneath the shrub. Traps under the *Grevillea* were the only ones to capture significantly less seed than the control traps. The Control traps were placed amongst established vegetation, so that there was a double advantage of abundant seed source close to the traps and structural obstacles to prevent the seeds from travelling very far once detached from the parent plant. The *Grevillea* traps on the other hand, were completely or almost completely covered by the shrub's prostrate branches, largely preventing seeds from reaching this microhabitat. The number of species dispersing to different microhabitats was also similar, with bare areas receiving comparable number of taxa to other microhabitats. Only *Grevillea* traps at Lake Botsford caught fewer species than those placed in control vegetation or at the edge of the prostrate shrub. Once again, access to this microhabitat could have been more of a problem for some seed types than others. This site also had the lowest number of seed rain taxa, but the greatest seed rain density, which could have amplified the differences.

Other authors have also documented uniform patterns of seed deposition within a habitat. Russell and Schupp (1998) found that there was no difference in initial *Cerocarpus ledifolius* seed numbers arriving under the canopy of shrubs and in the open interspaces between woody vegetation. However, sampling the top 3 cm of litter and soil revealed *Cerocarpus* seeds were fourfold more abundant beneath shrubs compared to open areas. Similarly, Aguiar and Sala (1997) working in the Patagonian steppe have shown that traps located in bare areas far from plants captured similar amount of *Bromus pictus* seeds to those located near shrubs or tussock grasses. Again, when the top 4 cm of soil and litter was examined, densities of *Bromus* seeds were up to nine fold higher under shrubs compared to open areas. Bare ground microsites retained very low numbers of seeds, and even then only if they were located nearer than 10 cm to a plant

or litter microsite (Aguiar & Sala 1997). Clearly, seed redistribution and accumulation occurs during secondary dispersal, so that relatively even seed densities among microhabitats become more heterogenous through time as vegetation hinders secondary movement of seeds. In both studies, bare patches lacked seeds in litter and topsoil because of their inability to retain them, not because no seed arrived there initially (Aguiar & Sala 1997; Russell & Schupp 1998).

This homogenous influx of seeds during primary dispersal is contrary to the seed trapping by plants observed by Bullock and Moy (2004). They reported 7-15 times more seeds within 10 cm of *Calluna vulgaris* and *Erica cinerea* bushes for allospecific deposition, and 8 to 20-fold higher densities for conspecific deposition compared to background seed numbers of those species in the surrounding short grassland vegetation. The authors argue that because the dry, pitfall-type seed traps were raised 1 cm from the ground, this acted as a barrier to ground saltation of seeds, and thus the deposition pattern reflected primary dispersal only, rather than seed accumulation over time. Wilby & Shachak (2000) also trapped more seeds in shrub patches compared with inter-shrub patches in an arid shrubland, but their sticky traps were level with the soil surface, thus presumably capturing both primarily and secondarily dispersed seeds. Tendency for higher seed numbers under clumps of shrubs have also been reported by Fuentes *et al.* (1984) in the Chilean matorral for five out of eight species trapped from seed rain, and all eight species in the seed bank, but no quantitative comparisons were made due to the small numbers.

In contrast, Grulke (1995) reported greater *Phippsia algida* seed rain on bare soil (90%) in High Arctic polar semidesert than in other microsites like moss (8%), and desiccation cracks (2%), with no seeds found within vascular plants. However, this pattern was likely influenced by the sticky nature of the algae-covered soil surface during seed dispersal, and the proximity of mature *Phippsia* plants to bare areas, as well as some difficulties with tracking seeds within vascular plant patches.

Spatially heterogenous deposition of seeds was also suggested by Reader and Buck (1986), who trapped more seeds of *Hieracium floribundum* at the top of depressions than at the bottom, but once again this could have been influenced by greater frequency of reproductive individuals at the top of the depressions.

All of the studies discussed above focused on only one species, yet Willson and Crome (1989) found that shrubs affected different seed types differently. While wind dispersed, plumed seeds of weedy herbs arrived in greater densities in the open than under shrubs, vertebrate-dispersed seed deposition was significantly higher under shrubs, and shrub microhabitats had no detectable effect on deposition of heavier, winged tree seeds, such as *Toona australis.*

In the absence of specific dispersal mechanisms, like plumes or other appendages, seed size could be equally important to deposition patterns. Although Grulke (1995) found that *Phippsia* seeds did not accumulate in desiccation cracks, such microtopographic features can function as seed traps during secondary dispersal for large seeds which are not easily incorporated into fine textured soil (Elberling 2000). Large seeds tend to move horizontally across small particle size soils, and not be trapped, while small seeds and seeds with adhesive seed coats are more easily trapped. Small seeds also reach greater depth in the soil column than large diaspores, or those with an adhesive coat (Chambers *et al.* 1991). This clearly has important implications for seed germination and species composition of establishing seedlings.

In a community level study, such as this one, many different types of seeds are trapped, and even when the seed rain is dominated by only a few species, as documented in this study and elsewhere (Marchand & Roach 1980; Stöcklin & Bäumler 1996; Urbanska *et al.* 1998; Urbanska *et al.* 1999; Wilby & Shachak 2000), the main contributors can be morphologically diverse. Consequently, the results might not be as unambiguous as when a single species is targeted. Individual species do not necessarily reflect the general pattern of dispersal, as illustrated here by *Grevillea* seeds amongst others. Total *Grevillea* seed densities were 6 fold higher in Edge traps than in Bare or Grevillea traps,

and 9 times higher than in control traps. *Grevillea* seeds are large and relatively heavy compared to most other species in the community, therefore its dispersal distances are likely to be much shorter than for wind dispersed, plumed seeds, or smaller, lighter seeds. In addition, vegetated patches containing control traps were often raised compared to eroded bare areas occupied by the prostrate *Grevillea,* limiting the arrival of this species in those microhabitats.

Understanding seed rain patterns could be further complicated by the trap design assuming only seeds in the primary stages of dispersal are collected. The traps were left out for a whole month in a very windy environment, so that a 1 cm high barrier might not have been sufficient to prevent some secondary movement and accumulation of seeds in the funnels, particularly in bare patches, where the traps could have fulfilled the function of desiccation cracks. As seeds fall into the traps, they are immobilised and no further transport occurs. In the absence of such artificial collection points, many seeds will continue to be dispersed until they encounter a natural obstacle, so a trap placed in a flat sandy bare patch could overestimate the amount of seed rain received in that type of microhabitat if microtopographic features are sparse. Furthermore, the projecting trap rim is not equally effective against the deposition of different seed types, with plumed, wind dispersed seeds more likely to be uplifted and dropped into the trap than heavier seeds without such appendages. Due to the windy environment and the low stature of many species, this problem is not easily solved with a different trap design or placement. Sticky traps, artificial turf, or water filled trays would have also provided an artificial anchorage or collection point for seeds in the secondary stage of dispersal. These considerations reinforce the importance of secondary dispersal– it is not enough for a seed to land in a particular microhabitat, it must also be retained there long enough to germinate.

Despite some limitations, this is the first study to quantify seed rain density and patterns of deposition in a shrubby alpine community in Australia. It demonstrated a long seed dispersal period from summer to late autumn, with pulsed inputs from individual species, and densities comparable to other alpine and shrubby areas. Primary seedfall

was uniform across the landscape, with vegetated and bare microhabitats receiving similar seed densities and numbers of species as well as suites of species. However, longer-term studies that cover a range of vegetation types are needed to understand between year seed rain variation. These studies should clearly distinguish between primary and secondary dispersal, and consider a shorter sampling interval during peak dispersal periods to minimise seed loss due to germination, predation and decay. Working in remote areas might make that a difficult task. Increasing the trapping area by increasing the number of units should also be considered, but the time required to process the samples should be kept in mind. Some further questions to investigate in the future, which were not addressed in this study, could include relative abundances of microhabitats, proximity to reproducing parent, and detailed analysis of seed size and dispersal mechanisms in the community. An assessment of the seed bank, and loss of seeds due to decomposition before they can germinate would also give a more complete picture of seed dynamics and the potential role of seed rain and seed bank in regeneration.

Chapter 5. Fate of seeds - Post-dispersal predation

INTRODUCTION

Post-dispersal seed predation has the potential to influence patterns of plant fitness, recruitment, population expansion and community structure (Andersen 1982; Hulme 1994; Auld & Tozer 1995; Hulme 1998; Wilby & Shachak 2000). Unless species are buffered by a large active seed bank, post-dispersal seed losses could have a significant impact on plant population processes (Hulme 1998). If regeneration is microsite limited rather than seed limited, however, seed predation is likely to play only a minor role in plant demography (Andersen 1989; Crawley 1992; Hulme 1998). Yet even when suitable microsites are rare, seed predators may influence competition for those microsites through differential mortality of seeds, and therefore seed predation could still be important not only in communities dominated by annuals, but those dominated by long lived perennials also (Hulme 1998).

Post-dispersal seed predation rates can be very high and extremely variable in space and time, with seed losses of up to 100 % not uncommon (Whelan *et al.* 1991; Crawley 1992; Hulme 1998), and exceeding those attributed to pre-dispersal seed predators (Auld & Denham 1999, 2001). Unlike the small, sedentary specialist insect feeders mostly involved in pre-dispersal seed predation, post-dispersal seed predators tend to be small mammals, rodents, and birds, as well as ants, which play a major role in some environments (see Crawley 1992 for numerous examples). Lygaeid bugs and carabid beetles have also been observed to remove seed (Cremer 1965 in Ashton 1979; Andersen 1985; Traveset 1990), although they are probably not as important post-dispersal seed predators as seed-harvesting ants, which are characterised by great

abundance as well as high level of activity and social organization which enables them to remove large amounts of seeds (Andersen & Ashton 1985).

Seed harvesting by ants (i.e. predation as opposed to myrmecochory where seeds with attractive elaisosomes are simply dispersed without being consumed) is largely a phenomenon of arid or seasonally arid regions of the world (Andersen 1991). In contrast, it is widespread throughout the Australian continent and is common in most major habitat types (Andersen 1991). Ants are exceptionally abundant and diverse in Australia (Majer 1983; Andersen 1991), and in most plant communities harvester ants are the major post-dispersal seed predators, recorded to remove seeds at high rates in almost all habitats studied (Andersen 1991). With the exception of a few groups of specialist granivores restricted to the arid zone, all harvesting ant species are omnivorous, feeding opportunistically on seeds, primarily from woody plants (Andersen 1991).

Ten Australian ant genera are known to contain seed-eating species; *Heteroponera*, *Mayriella* and *Solenopis* (represented by single, uncommon, or localised harvesting species), *Melophorus, Meranoplus*, and *Tetramorium* (most harvesting species restricted to arid regions), *Rhytidoponera* and *Prolasius* (harvesting species mostly confined to mesic southern and south-eastern Australia), and *Pheidole* and *Monomorium* (harvesting species throughout Australia) (Andersen 1991). Clearly, only the last four genera are likely to be encountered in Tasmania. Some omnivorous *Iridomyrmex* spp. are also recognized as potential seed-removers (Andersen 1982; Rudkin & Pickering 2002). Although seed harvesting by ants is thought unlikely to be important in Australian alpine regions, owing to relatively few ants in those habitats in general (Andersen 1991), there are no published studies investigating this. Yet, Muñoz & Arroyo (2002) reported that 14% of *Sisyrinchium arenarium* seed was removed by ants at 2 700 m elevation in the Central Chilean Andes compared to 4% by avian granivores, with only one species of each seed predator observed.

Post-dispersal seed predation in alpine communities has received little attention, in contrast to plant-pollinator interactions or herbivory, even though potential seed predators, such as rodents, are present in high altitude areas (Körner 1999), where seasonal or pulsed productivity is likely to make long-lived resources, such as seeds, appealing to primary consumers (Wilby & Shachak 2000). In general, despite the voluminous literature, our knowledge of post-dispersal seed predation and the impacts of different guilds of granivores is inadequate, particularly in habitats of the Southern Hemisphere (Hulme 1998). In addition, little is known about ant species (or other invertebrates) on the Central Plateau, and generalizations from other areas are not always informative, given that different vegetation types have distinctive ant assemblages (Andersen 1982). The aims of this study were therefore to determine if any potential seed harvesting invertebrate species occurred at the Central Plateau study sites, and to assess their role in post-dispersal seed removal, and hence plant regeneration in the area. Vertebrate granivores were not investigated.

METHODS

Pitfall traps

Pitfall traps were used to sample ground–dwelling invertebrates. Pitfall trapping is one of the most common and efficient methods for sampling small, surface active arthropods (Majer 1997; Melbourne *et al.* 1997). Ten pitfall traps were deployed per site (Lake Botsford and Carter Lakes), spaced every 5 m in two parallel transects which were located 10 m apart. Trap positioning along the transects reflected a variety of microhabitats available, including bare ground, low, thick vegetation cover, and proximity to large shrubs.

A pitfall trap consisted of a clear plastic 45 mm wide, 60 mm deep specimen jar, buried to soil level, and shielded with a 12 cm wide, round, clear plastic cover, suspended c. 5

cm above the jar with two metal tent pegs (Figure 5.1). The cover provided protection from debris, rain and animal disturbance, though not successfully enough in all cases. The plastic jar was one third to half filled with a mixture of preserving agent and evaporation retardant (70% ethanol and 30% ethylene glycol).

Sampling began 27 March 2002 at Lake Botsford and continued until 27 May, before re-commencing 30 November 2002 through to 20April 2003. At the Carter Lakes site, sampling was carried out only during the summer and autumn of 2002/2003 (30 November 2002 to 18 April 2003). The pitfalls were collected every 25 to 31 days (usually every 29 days) and replaced with fresh jars. This long interval between collections was due to logistical considerations, as shorter periods would have been preferable, but it ensured the disturbance caused by trap establishment and replacement ("digging in effect") was eliminated at collection time in the absence of permanent protective "sleeves" around the pitfall container. Pitfall traps were not deployed at Liawenee Moor, as there was already some data available from a previous study on invertebrate communities in and around the exclosures (Francis 1997).

Figure 5.1 Pitfall trap with shield *in situ* at Lake Botsford.

Once removed from the field, the trap content was sorted and the invertebrates were transferred into vials containing 80% ethanol for long-term storage and preservation. The specimens were identified to the level of order, with most being assigned to a family group, and in some cases to generic level. Taxonomic identification was carried out with the assistance of Dr Peter McQuillan, School of Geography and Environmental Studies, University of Tasmania. Although species level identification was not attained, higher taxon surrogacy or morphospecies identification has been shown to be equally accurate in estimating species richness and β diversity in studies of terrestrial invertebrates (Oliver & Beattie 1996; Pik *et al.* 1999; Báldi 2003).

Seed bait stations

In situ seed baiting experiments were conducted in conjunction with pitfall trapping. Ten 9 cm Petri dishes per site (Carter Lakes, Lake Botsford and Liawenee Moor Exclosures) were positioned along a 45 m transect, five meters apart, in a variety of microhabitats, including bare ground and dense vegetation. Three evenly spaced 15 mm access holes were cut in the perimeter of the clear dish and covered with the lid. A small rock was placed on top to prevent the lid from blowing off or birds and other vertebrates accessing the seeds. The gaps in the dish wall were wide enough to allow large ants and beetles to pass through and remove the seeds with ease, while protecting the seeds from removal by wind and rain (Figure 5.2). This design was modified from Andersen and Ashton (1985), who found that the construction had little effect on seed removal rates. Although it has been recommended that a range of seed sizes and morphologies be included per bait station (Andersen & Ashton 1985), difficulties with obtaining suitable seed in sufficient amounts meant that seeds of only three species found in the area were chosen for this study - *Orites revoluta, Orites acicularis*, and *Poa labillardieri* (Liawenee Moor only). Five seeds of each *Orites* sp. and a "pinch" of about 50 *P. labillardieri* seeds were placed inside the Petri dish and checked daily for up to six days, then left *in situ* between observation periods for the duration of the experiment. This monitoring process was carried out approximately once a month from late spring to early autumn, beginning at Liawenee Moor on 30 September 2002 (30 November 2002 at

Carter Lakes and Lake Botsford), and ending on 17 April 2003. This sample period presumably coincided with the highest invertebrate activity. The seeds were counted at each visit and any missing ones were replaced with fresh seed. Any damage or disturbance to the bait station was also noted and repaired.

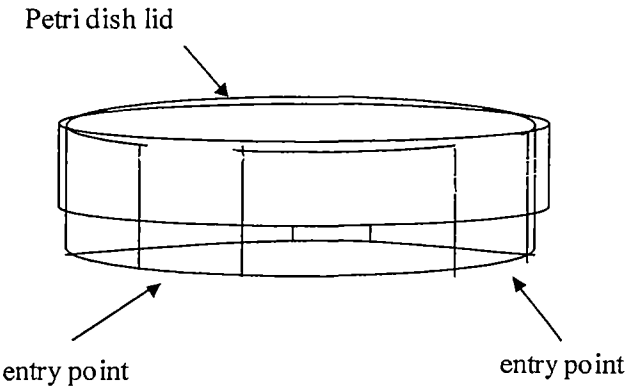


Figure 5.2 Diagram of bait station.

RESULTS

Pitfall traps

Between December 2002 and April 2003, pitfall trapping at Carter Lakes yielded 76 morphospecies from 62 families, 17 orders, and 6 classes of Arthropoda. At Lake Botsford, trapping in April and May 2002, and between December 2002 and April 2003, resulted in 68 morphospecies identified to 56 families, 16 orders, and 5 classes of Arthropoda, as well as a *Geoplana* sp. from the flatworm phylum Plathyhelminthes (see Table 5.1 for full species list). At Lake Botsford, the collections were dominated by ants (Hymenoptera: Formicidae), with over 75% of total catch represented by this family

alone (Figure 5.3). The remaining orders each contributed less than 6% of specimens caught, with six orders accounting for just 0.62% of the entire collection. The groups captured at Carter Lakes were more evenly represented, but ants still dominated, contributing over 25% of specimens caught (Figure 5.3). Acarina (mites), Araneida (spiders), Mecoptera (scorpion flies) and Diptera (flies) were also well represented at this site, with 16.9%, 11.9%, 10.7% and 10.3% of specimens respectively. Four potential seed eaters were identified at the two sites; *Conoderus* sp. (Coleoptera: Elateridae) was restricted to the Lake Botsford samples, while members of the Lygaeidae (Hemiptera), *Bobilla* sp. (Orthoptera: Gryllidae) and *Kinemania* sp. (Orhtoptera: Gryllacrididae) were found at both sites. However, the combined contribution of these species to the total numbers caught was less than 0.5% at Lake Botsford, and less than 3% at Carter Lakes. No members of seed harvesting ant genera were identified at either site, but a species of *Iridomyrmex*, which are usually general scavengers, were abundant at Lake Botsford, especially during summer (Figure 5.4). The mean number of all other specimens per trap also peaked in January at both sites (Figure 5.4). The relatively high values for April 2003 were due to large numbers of *Apteropanorpa* sp. and Opiliones captured that month at both sites.

Table 5.1 Carter Lakes and Lake Botsford Invertebrates. Potential seed eating species in bold. Total shows number of individuals, and % indicates the percentage of total invertebrates caught at each site over all sampling periods.

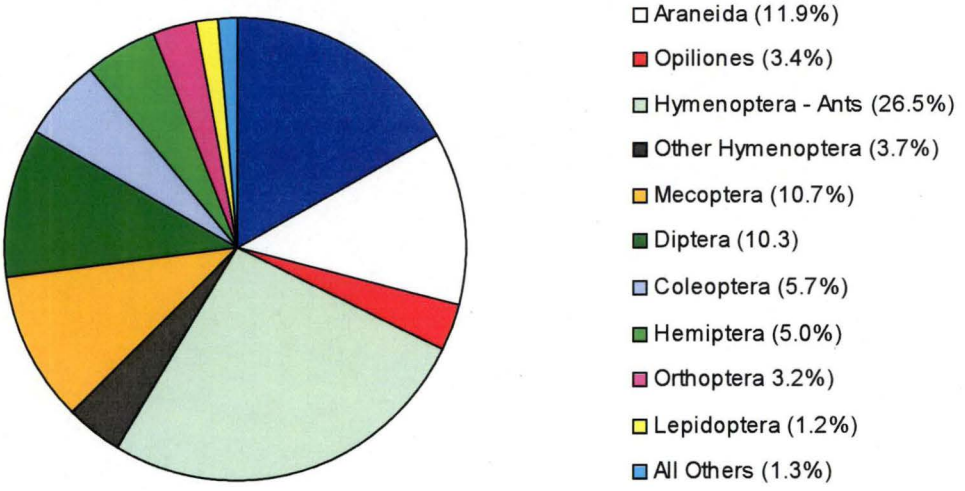
CLASS	ORDER	FAMILY	SPECIES	COMMON NAME	Carter Lakes		Lake Botsford	
					total	%	total	%
Arachnida	Acarina	Erythraeidae		red mite	124	16.40	213	5.54
		Oribatidae		soil mite	4	0.53	1	0 03
	Araneida	Anaurobiidae		spider	4	0.53		
		Gnaphosidae		spider	6	0.79		
		Lycosidae	*Artoria sp.*	wolf spider	30	3.97	45	1.17
			Lycosa sp	wolf spider	1	0.13	6	0.16
		Salticidae		jumping spider	10	1.32	11	0 29
		Thomisidae		spider			1	0 03
		Zodariidae		spider	2	0.26		
				trap door spider			1	0.03
				un-ided spiders	37	4 89	92	2.39

	Opiliones			harvestman	26	3 44	55	1.43
Chilopoda				centipede			2	0.05
Collembola				springtails	many		many	
Insecta	Blattodea	Blatellidae		cockroach	1	0.13	3	0.08
		Blattidae	*Platyzosteria sp.*	cockroach	1	0.13	1	0.03
	Coleoptera	Cantharidae	*Chauliognathus sp*	soldier beetle larva	1	0.13	67	1.74
		Carabidae	*Chylnus sp.*	beetle	1	0.13		
			Mecyclethorax?	beetle	1	0.13		
			Promecoderus sp	carabid beetle	8	1.06	30	0.78
			Scopodes sp	beetle	1	0.13		
			Tachys sp	beetle	3	0 40		
				truncate carabid beetle	1	0.13	3	0 08
				un-ided beetle larva	1	0.13		
		Curculionidae	*Poropterus sp*	weevil			1	0.03
				weavil	3	0.40	1	0.03
		Dermestidae		beetle larva	1	0.13		
		Elateridae	***Conoderus sp.***	**click-beetle**			**4**	**0.10**
		Lathridiidae		beetle	1	0.13		
		Leiodidae		beetle	1	0.13		
		Lucanidae	*Lissotes sp.*	stag-beetle	1	0.13	3	0.08
		Lycidae	*Metriorynchus sp.*	beetle larva	2	0.26	1	0.03
		Melyridae	*Hypattulus sp.*	beetle			2	0.05
		Pselaphidae		beetle	1	0.13	8	0.21
		Scarabaeidae	*Onthophagus australis*	dung beetle			5	0.13
			Heteronyx sp.	scarab beetle	1	0.13	1	0.03
		Scydmaenidae		beetle	1	0.13	3	0.08
		Staphylinidae		beetle	14	1.85	17	0.44
	Dermaptera	Anisolabididae	*Anisolabis sp*	earwig	1	0.13		
				earwig			2	0.05
	Diptera	Bombyliidae		bee-fly			1	0.03
		Calliphoridae		blow-fly	6	0.79	1	0.03
		Cecidomyiidae		gall midge fly	3	0.40	4	0.10
		Chironomidae		midge	3	0.40	28	0.73
		Chloropidae		grass-fly	3	0.40	6	0.16
		Culicidae		mosquito	1	0.13		
		Dolichopodidae		fly			2	0.05
		Muscidae		fly	7	0 93	8	0.21
		Mycetophilidae		fungus gnat	2	0.26		
		Phoridae		fly	40	5.29	32	0.83
		Sciaridae		mushroom-fly	2	0.26	15	0.39
		Tabanidae		march-fly	1	0.13		
		Tachinidae		fly	5	0.66	4	0.10
		Therevidae		fly	4	0.53		
		Tipulidae		fly	1	0.13		
	Hemiptera	Cicadellidae		leafhopper	25	3.31	13	0.34

		Cydnidae		bug	2	0 26		
		Lygaeidae		**seed-bug**	**8**	**1.06**	**4**	**0.10**
		Miridae		bug	2	0.26	5	0.13
		Psyllidae		psyllid	1	0.13	1	0.03
	Hymenoptera	Braconidae		wasp			1	0.03
		Chalcidae		wasp	5	0.66	1	0.03
		Formicidae	*Amblyopone sp.*	ant	1	0.13		
			Anonychomyrma sp	ant	95	12.57	39	1.01
			Hypoponera sp.	ant			4	0.10
			Iridomyrmex sp.	**ant**	**74**	**9.79**	**2854**	**74.17**
			Myrmecia sp.	Jack Jumper	27	3.57	36	0.94
			Ant sp. 2	ant	1	0.13		
			Ant Sp 3	ant	1	0.13	6	0.16
			Ant sp 4	ant	1	0.13		
			Ant Sp. 5	ant			1	0.03
			Ant Sp 6	ant			1	0.03
		Halictidae		native bee	1	0.13		
		Ichneumonidae		wasp	2	0.26	6	0.16
		Mutillidae		wasp	5	0.66	2	0.05
		Mymaridae		wasp			1	0.03
		Pompilidae		wasp	11	1.46	2	0.05
		Proctotrupidae		wasp	4	0.53	14	0.36
				un-ided wasp			10	0.26
	Lepidoptera	Arctiidae		moth	3	0.40		
		Geometridae		moth larva		0.13		
		Hepialidae		moth			1	0.03
		Noctuidae	*Dasygaster sp.*	moth	1	0.13	1	0.03
		Oecophoridae		moth	4	0.53	29	0.75
	Mecoptera	Apteropanorpidae	*Apteropanorpa sp.*	scorpion fly	81	10.71	87	2.26
	Orthoptera	Acrididae	*Phaulacridium sp*	grasshopper	5	0.66	1	0.03
			Tasmaniacris sp.	grasshopper	8	1.06	5	0.13
		Gryllidae	***Bobilla sp.***	**cricket**	**7**	**0.93**	**1**	**0.03**
		Gryllacrididae	***Kinemania sp.***	**cricket**	**4**	**0.53**	**7**	**0.18**
	Plecoptera			stone fly			1	0.03
	Psocoptera			book lice	1	0.13		
Malacostraca	Amphipoda			crustacean	1	0.13		
Symphyla				multipede	2	0.26	1	0 03
Turbellaria*	Tricladida	Geoplanidae	*Geoplana sp*	land planarian			33	0.86

*Phylum = Platyhelminthes (flat worms)

a) Carter Lakes - Invertebrates captured in pitfall traps



b) Lake Botsford - Invertebrates captured in pitfall traps

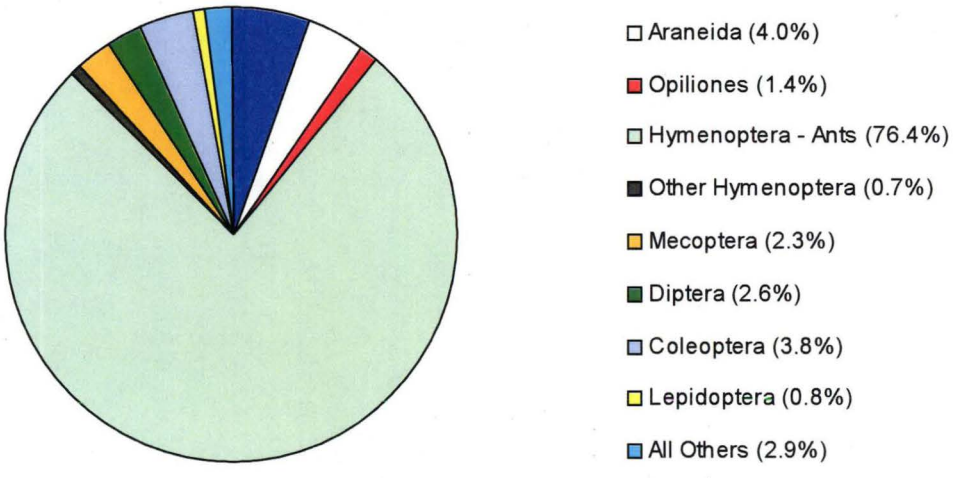


Figure 5.3 Pitfall composition excluding Collembola at a) Carter Lakes and b) Lake Botsford. (All Others at Carter Lakes include: Amphipoda, Diplopoda, Symphyla, Dermoptera, Blattodea, Psocoptera. At Lake Botsford: Orthoptera, Blattodea, Dermaptera, Plecoptera, Symphyla, Chilopoda, Hemiptera, Land Planarians).

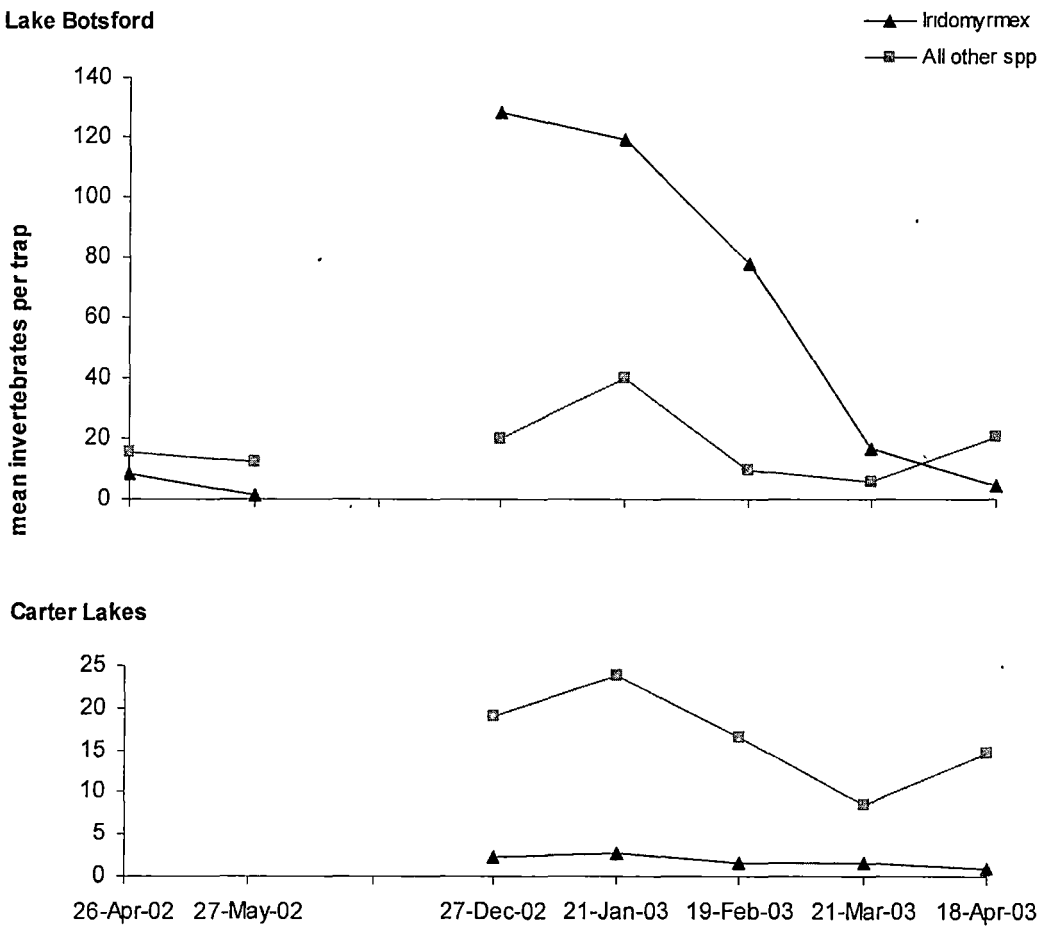


Figure 5.4 Average monthly pitfall catches at Carter Lakes and Lake Botsford. N=10, except January n=4.

Seed bait stations

No seeds appeared to be removed by ants or any other invertebrates from the bait stations over the course of the monitoring period. Occasionally one or two seeds were missing from the Petri dishes, but were always found adjacent to the bait station, with no sign of damage, and therefore they were presumably removed by wind or water. At no stage during monitoring were any invertebrates observed inside the Petri dishes or interacting with the seeds, even though ant activity was high in close proximity to the

bait stations during the summer months. Therefore, the data from this experiment is not presented here.

DISCUSSION

The bait station experiment failed to document seed removal over a period of five to seven months at the study sites. However, it cannot be stated conclusively that seed harvesting by invertebrates does not occur in the area. While large scale harvesting is unlikely due to the absence of seed-eating ant species, it is possible that omnivorous species like *Iridomyrmex* found in the pitfall traps could remove some seeds following primary dispersal. *Iridomyrmex* is one of the largest and most frequently encountered groups in Australia, and is a dominant genus in most Australian ant communities (Andersen 1991; Shattuck 1999). This genus has been previously observed to remove seeds from bait stations (Willis *et al.* 1997), and has also been proposed as a potential seed dispersal agent in the Kosciuszko alpine area (Rudkin & Pickering 2002).

The limited number of species used in the seed bait experiments could have affected the results. Andersen (1982) recommends that a range of seed types be included in "cafeteria-style" experiments, as ants show considerable seed species selectivity, and therefore the results from one plant species should not be generalized to others (Brown *et al.* 1975; Briese & Macauley 1981; Andersen & Ashton 1985; Andersen *et al.* 2000). Only three seed species were used in this study, two of them from the same genus, displaying no significant difference in morphology or size. The choice of bait material was limited, dictated by seed availability of local species during the study. *Orites revoluta* and *O. acicularis* are ecologically important, dominant species in the environment, and thus were appropriate choices to investigate whether post-dispersal seed predation by arthropods was influencing colonisation of bare patches. Although *Grevillea australis* is also a dominant, widespread species at the study sites, the large

hard-coated seed was deemed less likely to be appealing to invertebrates. Both *Orites* species have seeds with a brittle, papery wing, similar to those of *Grevillea pteridifolia* which have been reported to be readily taken by ant genera that are seed predators, as well as elaiosome collectors, including *Iridomyrmex* spp. (Majer & Lamont 1985). The bait stations at Liawenee Moor did have two very different types of seeds per station (*Poa* and *Orites* seeds), and yet the seeds were not removed either. Considering that seeds eaten by harvesting species of ants in Australia are often from woody plants rather than primarily from grasses or herbaceous species (Andersen 1991), adding more herbaceous seeds to the bait stations was not necessarily going to increase the chances of seeds being removed if harvesting ant groups were present in the area but somehow avoided capture in pitfall traps.

In comparative studies of sampling methods, Majer (1997) found that pitfall trapping never obtained more than 60% of ant species from the more complete sample set. Longer term trapping surveys may also be needed to detect some species. In a woodland study at Mt Piper, Victoria, three to five fortnightly sampling occasions were sufficient at most sites to capture approximately 75% of species present, but at one site this target was not achieved even after 10 sampling periods over seven months (Hinkley & New 1997). Pitfall traps may not be effective for species associated with soil, deep litter and vegetation and used alone provide a skewed representation of the ant functional groups, e.g. cryptic hypogaeic ants, rare ants or those with sparse distribution and low numbers (Majer 1997). This problem becomes more pronounced with increasing structural complexity of the habitat, as in general, trapability not only of ants, but other groups like crickets, increases as the habitat becomes more open (Majer 1997; Melbourne *et al.* 1997; Melbourne 1999). Adequate numbers of suitable sized traps might overcome this problem to some extent for surface-active ant communities and other invertebrate taxa (Majer 1997).

Pitfall trapping has its limitations, and the size of the trap, the preserving material used, and the arrangement of the traps could have biased the results against some groups and in favour of others (Luff 1975; Spence & Niemelä 1994; Trueman & Cranston 1997).

They are nevertheless convenient, simple to use, can operate continuously for extend periods, are inexpensive and labour-efficient, and catch enough arthropods for rigorous statistical analysis (Spence & Niemelä 1994; Majer 1997).

The limitations of surveying invertebrates via pitfall trapping aside, the timing of the seed baiting experiments could have also been a problem. Andersen & Ashton (1985) recommend that seed baiting studies should be carried out at the time of natural dispersal, and therefore seed availability, to reflect natural rates of removal, as removal rates by ants vary widely across seasons. Foraging by some species has been reported to slow down in winter, or for species to go dormant in the cooler months (Ashton 1979; Majer 1983; Hinkley & New 1997; Miller & New 1997). Although the baits were maintained until late April, *Orites* seeds are just beginning to disperse at this time and are still available in late May. It is possible that ant and invertebrate activity in general ceases markedly by this time so no harvesters are available to remove the seeds. Indeed, pitfall captures of *Iridomyrmex* sp. were much lower during April and May than in December, January and February. During the warmer months when activity is high, there might be other, more preferable food sources available to the omnivores, making them even more selective in regard to seed species harvested. Wilby & Shachak (2000) observed this to be the case with harvester ants in an arid shrubland in the Negev Desert. Seed removal by ants can also be extremely variable in a small area of apparently uniform vegetation, with only some of the baits located and only a percentage of the seeds removed (Brown *et al.* 1975; Andersen 1982; Abramsky 1983; Mittelbach & Gross 1984; Miller & New 1997). The seed bait stations were operational for sufficiently long periods of time to be located by any foraging invertebrate, especially ants, as previous studies documented seed removal within a few days, mostly during the first day (Andersen 1982) or within a week (Ashton 1979), and a maximum of 10 days bait exposure was recommended by Andersen & Ashton (1985).

There is no doubt that ants are important post-dispersal seed predators in most Australian systems (Andersen 1982; Andersen & Ashton 1985; Andersen 1987, 1991), but studies investigating their role in alpine areas are lacking, based on the assumption

that seed harvesting is unlikely to occur in high altitude environments (Andersen 1991). A search of the literature revealed only two alpine studies, conducted in the Central Chilean Andes. Muñoz & Arroyo (2002) reported 14% seed removal by ants in the subandean scrub zone at 2700 m, compared to 2% removal by avian granivores. However, only one species *(Sisyrinchium arenarium)* was used in those trials over a 10 day period in mid autumn when foraging activity might have been lower than earlier on in the season, but which corresponded to advanced seed dispersal for many species in the area (Muñoz & Arroyo 2002). Ants also removed up to 24% of *Chuquiraga oppositifolia* seeds, an Asteraceae dwarf shrub, in another experiment in the Central Chilean Andes during March and April (Muñoz & Cavieres 2006), so clearly this invertebrate group could be affecting seed availability of at least some species in alpine systems.

The other potential seed-eaters detected in pitfall traps, a Lygid bug, *Conoderus* sp., *Bobilla* sp. and *Kinemania* sp., might not have located the baits due to low numbers or sparse distribution of these groups, or the seed selection was not appealing to those species either.

Seed predation by small mammals and birds has not been the subject of this study, but could account for some seed losses on the Plateau, as vertebrates are often the most important seed predators in many habitats outside Australia (Whelan *et al.* 1991; Hulme 1994; Anderson & MacMahon 2001; Saba & Toyos 2003; Kelt *et al.* 2004). Although mammals are not generally regarded as important seed predators in Australia, Vaughton (1998) found on average 92% of *Grevillea barklyana* seeds were removed by rodents from coastal heath and woodland sites during late spring and early summer. Furthermore, Auld and Denham (1999) working in south-eastern Australia found that native rodents (*Rattus fuscipes)*, and macropods (*Wallabia bicolor)*, were responsible for annual seed losses of between 82 and 95% in four species of *Grevillea* lacking an elaiosome. Those rodent and macropod species are absent in Tasmania, but analogous species in the Central Plateau area include the long-tailed mouse (*Pseudomys higginsi*), whose diet includes fungi and invertebrates, as well as seeds and fruit, and possibly the

swamp rat (*Rattus lutreolus*) (Watts 1993). The house mouse (*Mus musculus*), one of three introduced rodents in Tasmania, which feeds predominantly on plants and seeds and is reportedly widespread in native vegetation (Watts 1993) and has been reported in the vicinity of the study sites, could also be consuming a variety of seeds in the area. Le Roux (2002) found seeds and inflorescences of *Acaena magellanica* to be consumed throughout the year by *Mus musculus* on subantarctic Guillou Island (Kerguelen archipelago), being the preferred diet during the summer months, with some evidence of seed storage for consumption during winter. Seeds of *Poa annua* and *Taraxacum officinale* were also taken. The other two introduced rodents, black rat (*Rattus rattus*), and brown rat (*Rattus norvegicus*), could also consume and cache seeds, but their presence around the study sites has not been verified (Watts 1993).

About 11 species of birds found around the Liawenee/Lake Augusta/Central Plateau Conservation area are predominantly seed eaters, and a further 10 have been recorded to consume seeds amongst other mostly animal material, including seeds of species found in the area (Table 5.2). Most of these species were regarded as common in the area in the past (Wall 1972). As with rodents however, a large proportion of the seed could be consumed prior to dispersal from the parent plant, or in the form of fruit.

Table 5.2 Bird List of potential seed eaters from Liawenee/Lake Augusta / Central Plateau Conservation Area. *Listed as common in the area by (Wall 1972).

Common Name	Species	Diet
Tasmanian Native-hen*	*Gallinula mortierii*	Seeds, leaves and vegetation and few insects. Seeds of *Senecio*, *Stellaria media* (Marchant & Higgins 1993) Seeds of *Juncus*, Poaceae, *Taraxacum*, *Cerastium*, *Scleranthus*, *Acaena* (Barker & Vestjens 1989)
Green Rosella*	*Platycerus caledonicus*	Mainly seeds of grasses, shrubs or trees, especially eucalypts, also fruits, flowers, nectar and insects and their larvae. Seeds of *Senecio*, *Poa*, *Ranunculus*, *Stellaria media*, berries of *Cyathoides* and *Coprosma* (Higgins 1999)
Blue-winged Parrot*	*Neophema chrysostoma*	Mainly seeds of grasses and herbaceous plants, also flowers, fruit and occasionally spiders. Seeds of *Senecio lautus*, *Astroloma humifusum* berries (Higgins 1999)

Long-billed Corella	*Cacatua tenuirostris*	Seeds of grasses, especially of cereal crops and herbaceous plants, as well as corms, bulbs and roots, also some insects. Seeds of *Brachyscome, Cerastium, Astroloma* (Higgins 1999)
Sulphur-crested Cockatoo	*Cacatua galerita*	Seeds of grasses and herbaceous plants, also fruits, flowers, bulbous roots and insect larvae. Asteraceae flowering heads(Higgins 1999)
Common Bronzewing*	*Phaps chalcoptera*	Wide variety of seeds and berries, especially *Acacia* (Frith 1984) Seeds, occasionally leaves and some invertebrates (Higgins & Davies 1996)
Brush Bronzewing	*Phaps elegans*	Seeds, including Epacridaceae, *Geranium, Ranunculus* (Higgins & Davies 1996)
Beautiful Firetail	*Stagonopleura bella*	Entirely small seeds on the ground (Frith 1984) , including Poaceae (Barker & Vestjens 1989)
Goldfinch*	*Carduelis carduelis*	Mainly seeds (Frith 1984), including *Juncus*, Poaceae, and many Asteraceae (Barker & Vestjens 1989)
Greenfinch	*Carduelis chloris*	Seeds (Frith 1984) Seeds and *Leucopogon* berries (Barker & Vestjens 1989)
House sparrow	*Passer domesticus*	Seed eater (Frith 1984) , including Poaceae and Asteraceae (Barker & Vestjens 1989)
Latham's Snipe*	*Gallinago hardwickii*	Omnivorous, seeds and other plant material, earthworms, spiders and insects. Seeds of *Juncus, Ranunculus*, Poaceae, *Brachycome, Epacris* (Higgins & Davies 1996)
Richard's Pipit*	*Anthus novaeseelandiae*	Some small seeds (Frith 1984) , but mostly insects (Barker & Vestjens 1989)
Starling*	*Sturnus vulgaris*	Omnivorous (Frith 1984) Seeds of *Astroloma humifusum*, but mostly animal material (Barker & Vestjens 1989)
Skylark*	*Alauda arvensis*	Possibly seeds (Frith 1984) , including *Festuca* (Barker & Vestjens 1989)
Grey Currawong	*Strepera versicolor*	Mostly animals, *Leucopogon* berries (Barker & Vestjens 1989)
Black Currawong*	*Strepera fuliginosa*	Mostly animals, *Cyathoides parvifolia* seeds and berries (Barker & Vestjens 1989)
Forest Raven*	*Corvus tasmanicus*	Mostly animals, Poaceae, *Epacris* seeds, (Frith 1984)
Silvereye*	*Zosterops lateralis*	Insects, nectar and fruit - native and introduced (Barker & Vestjens 1989) *Leucopogon* (seed, flowers, berries), *Coprosma* fruit (Barker & Vestjens 1989)
White-browed/ Tasmanian Scrubwren*	*Sericornis humilis*	Mostly insectivorous (Frith 1984) Mostly animal matter, also seeds of Poaceae, *Leucopogon, Geranium* (Barker & Vestjens 1989)
Superb blue/fairy Wren*	*Malurus cyaneus*	Occasionally takes small seeds (Frith 1984) , including *Geranium*, but mostly animal matter (Barker & Vestjens 1989)

Although the extent of post-dispersal seed predation on the Central Plateau invites further research, this study has found little evidence of invertebrate involvement in that process, while providing important baseline data relevant to arthropod diversity in the

area. Clearly, questions regarding the potential roles played by other taxonomic groups, and any seasonal variations in seed removal, or the full range of plant species involved remain to be explored. Although a large number of invertebrate taxa were active throughout summer and autumn, very few were identified as having the potential to be seed predators or harvesters. No seeds were removed at any of the three sites during baiting experiments, which were timed to coincide with high seed fall and invertebrate activity. Consequently, post-dispersal seed predation by invertebrates is unlikely to have a substantial impact on regeneration of bare patches. It is possible however, that seeds of select species not examined in this study are targeted by abundant groups such as *Iridomyrmex* sp. which could affect their potential colonisation of available microsites.

Chapter 6. Fate of seeds – Germination

INTRODUCTION

Although seed predation and loss of viability following dispersal can be significant, most studies suggest that germination is often the principal cause of seed depletion from the soil (references in Murdoch & Ellis 1992; Jansen & Ison 1995; Lunt 1995). Seed germination is a critical phase in the life history of sexually reproducing plants, and along with seed production, dispersal, and predation, the study of germination potential is essential to understanding colonisation processes and primary succession. For germination to occur, certain environmental requirements must be met to ensure favourable conditions for seedling emergence and establishment. Within a habitat, there may be more than one germination pattern responding to one or more environmental cue, so that some species germinate as soon as they are shed, while seeds of others remain dormant in the soil germinating intermittently or after a period of time (Angevine & Chabot 1979; Murdoch & Ellis 1992). Rapidly germinating seeds are at a lower risk of mortality from predation or pathogens, as well as having a competitive advantage over later-emergers (Angevine & Chabot 1979). Consequently, postponing germination beyond the first opportunity must confer a survival advantage on the seedling (Angevine & Chabot 1979).

In an ecological context, dormancy is an important germination strategy which delays or prevents germination, either as a result of inherent or external factors, allowing a species to avoid certain risks to seedling survival. Harper (1957 in Angevine & Chabot 1979) introduced a classification system that defined three types of dormancy: innate dormancy, induced dormancy, and enforced dormancy. Innate dormancy, also termed primary dormancy, is the inability of freshly shed seeds to germinate under favourable conditions. Induced dormancy, also termed secondary dormancy, is due to a particular

set of environmental conditions which may prevent germination. Enforced dormancy is maintained by an on-going unfavourable environmental state.

Tolerance of unfavourable seedling conditions, such as drought or low temperatures, is an alternative germination response, and usually involves high maternal investment in seed number or size to overcome mortality risks (Angevine & Chabot 1979). Avoidance of conditions which make seedling survival uncertain is the most common strategy however, and many species avoid drought by germinating predominantly in lower temperatures when soil moisture is more reliable, or escape cold conditions by germinating only after a period of very low temperatures (Angevine & Chabot 1979).

Australian species tend to germinate under temperatures that coincide with the annual period of reliable rainfall in their native habitat (Morgan 1998; Bell 1999; Schuetz *et al.* 2002; Clarke & Davidson 2004; Cooper *et al.* 2004), but it is common for some individuals in a population to be deeply dormant and delay germination in case the rainfall episode which promoted germination is inadequate for subsequent seedling survival (see examples in Bell 1999). Periods of higher, reliable rainfall often follow equally seasonal fire events, which are integral to many Australian environments. The influence of factors associated with fire on germination patterns of many native species is well documented, with thermal shock and smoke often having a promotive and synergistic effect on seed germination in a variety of habitats (*inter alta* Roche *et al.* 1998; Enright & Kintrup 2001; Hill & French 2003; Tang *et al.* 2003; Williams *et al.* 2005).

Despite recent expansion of research into the germination ecology of Australian native species in diverse environments (for example Bell *et al.* 1999; Read & Bellairs 1999; Tieu *et al.* 1999; Clarke *et al.* 2000; Gilmour *et al.* 2000; Brown *et al.* 2003; Allan *et al.* 2004), essentially nothing is known about the processes affecting germination and recruitment of shrubs or herbaceous species in alpine and subalpine zones of mainland Australia and Tasmania, or of the southern hemisphere in general (Baskin & Baskin 1998). There are no published accounts of germination or general seed ecology for any

of the species examined here. The aim of this study was therefore to compare temperature-dependant germination patterns, and thus gauge germination potential at different times of the year in a selection of dominant or common shrub and herbaceous species occurring in the Central Plateau area. The germination characteristics of each species could not only be indicative of their colonization potential of bare patches, but could also prove valuable in formulating active revegetation programmes.

METHODS

Seed collection

Seeds of the dominant shrubs common to all study sites (*Ozothamnus hookerii, Grevillea australis, Orites revoluta*, and *O. acicularis*) were collected at maturity and dried at room temperature for one to 12 months. Some *G. australis* collections were refrigerated for either 15 or 25 months after collection. In addition, seeds of five herbaceous species occurring at all of the study sites (*Acaena novae-zelandiae, Oreomyrrhis ciliata, Geranium sessiflorum, Ranunuculus pascuinus, Craspedia coolaminica*) were also harvested and stored in paper envelopes at room temperature for three weeks to four months prior to testing. The only grass species collected, *Poa gunnii*, was refrigerated for 2.5 years before germination trials commenced. Storage times were dictated by logistics and germination cabinet availability. Collections were carried out from late January to late May in 2001, 2002, 2003 and 2004 at Liawenee Moor, Bernacchi, and Carter Lakes sites (see Figure 1.5). Seeds were collected from many individuals to avoid overharvesting from a single plant, so that the harvest area and number of plants sampled varied depending on the species.

Treatments

All species were exposed to two temperature regimes. The treatments aimed to reflect *in situ* spring/autumn and summer surface air temperatures, with a "cold" cabinet alternating between 3 and 15°C (Spring/Autumn), and a "warm" cabinet alternating between 8 and 25°C (Summer) at 12 h intervals. The 12 hours of low temperature in each cabinet (3 or 8°C) coincided with 12 hours of darkness, and the 12 hours of high temperature (15 or 25°C) coincided with 12 hours of light (provided by 16 L40 W/ 20S cool white fluorescent tubes, delivering photosynthetic photon flux density of approximately 100 μmol m^{-2} s^{-1} at the surface). Some species were subjected to additional treatments in both temperature regimes, including cold stratification (2 or 8 weeks), exposure to smoke and heat, and dark incubation. These were applied singly or in combination. The number of replicates and seeds tested depended on the amount of seed available and seed size (Table 6.1). Germination was defined as the emergence of the radicle or the cotyledons through the seed coat.

Alternating temperature regimes

Three replicates of 50 seeds were assigned to each temperature regime (3/15 °C or 8/25°C). The species examined included *Grevillea australis, Ozothamnus hookerii,* and *Acaena novae-zelandiae* (3 month old seed), as well as *Orites acicularis* and *O. revlouta* (12 month old seed). There was only enough seed for two replicates of *Ozothamnus hookerii* in the warm treatment. Seeds were placed in 9 cm diameter Petri dishes on Wattmans No1 filter paper (9 cm diameter), over a 1 cm layer of vermiculite to which 15 mL of distilled water was added. The dishes were sealed with parafilm to prevent moisture loss, placed in their respective cabinets and checked daily during high germination periods and every two to seven days at other times. Germinated seeds were counted and removed, and more water was added if necessary. To avoid position effects, the Petri dishes were rearranged at random every few days after examination. Seeds were incubated for 151 days. The viability of ungerminated seeds at the end of the incubation period was not verified in this experiment, and therefore germination

percentages are based on total rather than viable seed numbers. However, all the seeds chosen appeared mature, healthy and entire. Despite this, all *G. australis* seeds were eventually lost to fungal infection before the end of the experiment. The use of fungicide on native species is not recommended (Baskin & Baskin 1998), so its use was avoided here. Seeds of the remaining species did not show signs of fungal infection.

In an additional experiment with herbaceous species, three replicates of 50 seeds of *Ranunculus pascuinus* and *Craspedia coolaminica* were assigned to each temperature regime (3/15°C or 8/25°C). There was only enough *Oreomhyrris ciliata* seed for three replicates of 45 per treatment, and even less *Geranium sessiliflorum* seed, with only three replicates of 15 seeds per cabinet. The seeds were collected in early February 2004 after a considerable amount of dispersal has already taken place and neither of the two species was as common at the site as *R. pascuinus* or *C. coolaminica*. After three weeks of dry storage at room temperature, the seeds were treated as in the previous experiments. Seeds were incubated for 112 days. At the end of the incubation period, the viability of ungerminated seeds was assessed by peeling back or removing the seed coat; those with a firm, white, healthy embryo were deemed viable. Dead seeds were excluded from the calculation of germination percentages in this experiment.

Cold stratification and alternating temperature regimes

Five replicates of 30 seeds were assigned to each temperature regime (3/15°C or 8/25°C), as 50 relatively large seeds per Petri dish proved too crowded. The species included *G. australis* (15 month old seed), *A. novae-zelandiae* (4 month old seed), *O. acicularis,* and *O. revoluta* (1 month old seed), and *Poa gunni* (2.5 year old seed). The seeds were treated as above, but refrigerated for two weeks at 4°C before being transferred to their respective cabinets. Seeds were incubated for 110 days, extended to 135 days for *O. revoluta* in the warm treatment, as it was still germinating in all replicates at day 110. The viability of ungerminated seeds at the end of the incubation period was not verified in this experiment either. Once again, all *G. australis* seeds were lost to fungal infection.

Effect of pre-treatments on G. australis *and* O. acicularis

The literature on the germination of other *Grevillea* spp. suggests that members of this genus respond to either smoke or heat treatments, and applying both often had synergistic germination promoting results (Edwards & Whelan 1995; Vaughton 1998; Kenny 2000; Morris 2000; Pickup *et al.* 2003). Seed coat scarification or complete removal has also resulted in successful germination (Howard 1963; Edwards & Whelan 1995). However, due to fungal problems encountered in previous trials, a scarification treatment was not initially included. Removal of the seed coat entirely was unlikely to occur in the field, and therefore a de-coating treatment would not have been reflective of germination *in situ.*

Four replicates of 40 one month old *G. australis* seeds (stored at room temperature since collection), and four replicates of 40 25 month old seeds (refrigerated since collection) were assigned to each treatment. Control seeds were soaked in 50 mL of distilled water for approximately 24 h, in uncovered glass beakers. Heat treated seeds were exposed to 80°C for 10 minutes in an oven prior to being soaked in distilled water as per control seeds. This temperature was within the optimum range for heat effects on many species without being lethal (Auld & Tozer 1995; Kenny 2000). Smoke treated seeds were soaked for approximately 24 h in uncovered beakers in a solution of commercial smoke water (Smokemaster 2000) and distilled water at 1:10 dilution. Where heat and smoke treatments were applied to the same set of seeds, heat exposure was followed by soaking in smoke solution. Any seeds which floated to the surface were replaced. The seeds were then placed in 9 cm diameter Petri dishes on Wattmans No1 filter paper (9cm diameter), and moistened with distilled water. The dishes were sealed with parafilm to prevent moisture loss, placed in their respective cabinets, and checked every 2 days to count and remove germinated seeds, and add more water if necessary. At the first sign of fungal presence, the seeds were sprayed with a dilute Benlate solution (0.5mg/L) to prevent loss of seed as in previous experiments. It has been previously applied to other *Grevillea* species which also had problems with fungal infections despite a number of precautions (Morris 2000; Pickup *et al.* 2003). All dishes had to be sprayed with Benlate eventually, but the smoke treated seeds appeared the most resistant to fungal

infection. The experiment using 25 month old seeds commenced six weeks into the incubation of the month old seeds which were already affected by fungal infection, so the filter papers were moistened with dilute Benlate solution from the start. This was effective in minimising and retarding the onset of the fungal infection, and Benlate solution instead of distilled water was sprayed to maintain moisture levels in all dishes. The seeds were incubated for nine months. After seven months without germination, and because fungal growth was minimised with Benlate, the two year old seeds were abraded with silicone carbide waterproof sand paper until the cotyledons were visible. This method was preferable to making an incision in the seed coat, as the chances of damaging the embryo were reduced. One month old seeds were incubated for a total of 292 days, and the 25 month old seeds were incubated for 275 days. Viability was not determined at the conclusion of the experiment.

Orites acicularis did not germinate successfully from one month old seed subjected to two weeks of cold stratification and either warm (8/25°C) or cold conditions (3/15°C) after 110 days, or from one year old seed under either of the temperature regimes after 152 days. Therefore, additional experiments were carried out. Three replicates of 25 seeds were subjected to smoke and heat treatments as for *G. australis* seeds, but only smoke, heat, and control conditions alone were tested. Petri dishes were divided into cold stratified and non-stratified treatments. Cold stratified treatments were refrigerated for eight weeks and subsequently transferred to the warm and cold growth cabinets. To minimise moisture loss and the need for topping up the dishes with water even further, they were grouped by temperature regime and placed in clear snaplock bags prior to placement in the fridge or growth cabinet (Figure 6.1). Half the dishes were wrapped in aluminium foil to assess dark germination, as the seeds are relatively large and might need some degree of burial prior to germination. The seeds were checked every seven days to count and remove germinated seeds, and add more water if necessary. Petri dishes in the dark treatment were not checked until the conclusion of the experiment at 195 days. Seed viability was not determined at the end of the experiment.

Table 6.1 Summary of species used and germination treatments applied.

Species	Collection Date	Storage	Length of storage	Treatments applied	Replicates x seeds	Duration
Ozothamnus hookerii	19/02/2003	room temp	3 months	Cold (3-15 °C)	3 x 50	152 days
	20/02/2003	room temp	3 months	Warm (8-25° C)	2 x 50	152 days
Orites revoluta	25/05/2002	room temp	12 months	Cold (3-15 °C)	3 x 50	152 days
				Warm (8-25° C)	3 x 50	152 days
	25/05/2003	room temp	1month	Cold (cold stratified for 2 weeks)	5 x 30	115 days
				Warm (cold stratified for 2 weeks)	5 x 30	135 days
Orites acicularis	26/05/2002	room temp	12 months	Cold (3-15 °C),	3 x 50	152 days
				Warm (8-25° C)	3 x 50	152 days
	25/05/2003	room temp	1 month	Cold (cold stratified for 2 weeks)	5 x 30	110 days
				Warm (cold stratified for 2 weeks)	5 x 30	110 days
	08/05/2004	room temp	1 5 months	Cold (3-15 °C) LIGHT (C, S, H)	3 x 25	196 days
				Cold (3-15 °C) DARK (C, S, H)	3 x 25	196 days
				Cold (3-15 °C) STRATIFIED 8 wks LIGHT (C, S, H)	3 x 25	196 days
				Cold (3-15 °C) STRATIFIED 8 wks DARK (C, S, H)	3 x 25	196 days
				Warm (8-25° C) LIGHT (C, S, H)	3 x 25	195 days
				Warm (8-25° C) DARK (C, S, H)	3 x 25	195 days
				Warm (8-25° C) STRATIFED 8 wks LIGHT (C, S, H)	3 x 25	195 days
				Warm (8-25° C) STRATIFED 8 wks DARK (C, S, H)	3 x 25	195 days
Grevillea australis	20/02/2003	room temp	3 months	Cold	3 x 50	152 days
				Warm	3 x 50	152 days
	11/03/2002	fridge	15 months	Cold (cold stratified for 2 weeks)	5 x 30	110 days
				Warm (cold stratified for 2 weeks)	5 x 30	110 days
	03/03/2004	room temp	1 month	Cold (S, H, S+H, C)	4 x 20	292 days
				Warm (S, H, S+H, C)	4 x 20	292 days
	06/03/2002	fridge	25.5 months	Cold (S, H, S+H, C),	4 x 20	275 days
				Warm (S, H, S+H, C),	4 x 20	275 days
Acaena novae-zelandiae	20/02/2003	room temp	3 months	Cold	3 x 50	152 days
				Warm	3 x 50	152 days
			4 months	Cold (cold stratified for 2 weeks)	5 x 30	110 days
				Warm (cold stratified for 2 weeks)	5 x 30	110 days
Poa gunni	27/01/2001	fridge	29 months	Cold (cold stratified for 2 weeks)	3 x 50	110 days
				Warm (cold stratified fro 2 weeks)	3 x 50	110 days
Oreomyrrhis ciliata	03/02/2004	room temp	3 weeks	Cold	3 x 45	112 days
				Warm	3 x 45	112 days
Geranium sessiflorum	03/02/2004	room temp	3 weeks	Cold	3 x 15	112 days
				Warm	3 x 15	112 days
Ranunculus pascuinus	03/02/2004	room temp	3 weeks	Cold	3 x 50	112 days
				Warm	3 x 50	112 days
Craspedia coolaminica	03/02/2004	room temp	3 weeks	Cold	3 x 50	112 days
				Warm	3 x 50	112 days

Figure 6.1 Seeds in Petri dishes with snaplock bags in germination cabinet.

Data analysis

Differences in mean final germination percentages, mean germination rate during the first week, and the average number of days taken to 50% of maximum germination were analysed using a single factor ANOVA with cabinet temperature the fixed effect in all cases. Where needed, the values were arcsine transformed prior to analysis to improve heterogeneity of variances which were checked using Cochran's test (untransformed data appears in all tables and figures). If the homogeneity of variances test was not met, type 3 T test was used to compare the two temperature treatments. Time taken to first germination was also calculated. All calculations exclude any moist chilling pre-treatment time and were performed in Microsoft Excel 2000.

RESULTS

Although final germination in both temperature treatments was generally high (over 80%) for most species, not all species germinated successfully. *Geranium sessiliflorum*, *Orites acicularis* and *Grevillea australis* all had mean final germination of less than 3% and therefore the data for those species is not presented. *Grevillea australis* seeds in most treatments were eventually lost to fungal infection. At the other extreme, *Poa gunnii* germinated almost completely (above 90%) during two weeks of cold stratification, and reached a mean maximum of 98% in both treatments after only four days in the growth cabinets. The data for this species is therefore not presented here either.

Alternating temperature regimes

Final germination percentages were not significantly different between the "spring/autumn" and "summer" treatments for most species tested (Figure 6.2 to Figure 6.5), with average germination between 85.3 ±4.8 % (cold treatment *A. novae-zelandiae*) and 100% (warm treatment *R. pascuinus* and cold treatment *C. coolaminica* and *O. ciliata*). One exception however, was *Ozothamnus hookerii* (Figure 6.4), with significantly higher mean germination in the warm treatment (40±10 %) than under the cold regime (4.7±1.8 %, $F_{1,3}$=20.55, P=0.02).

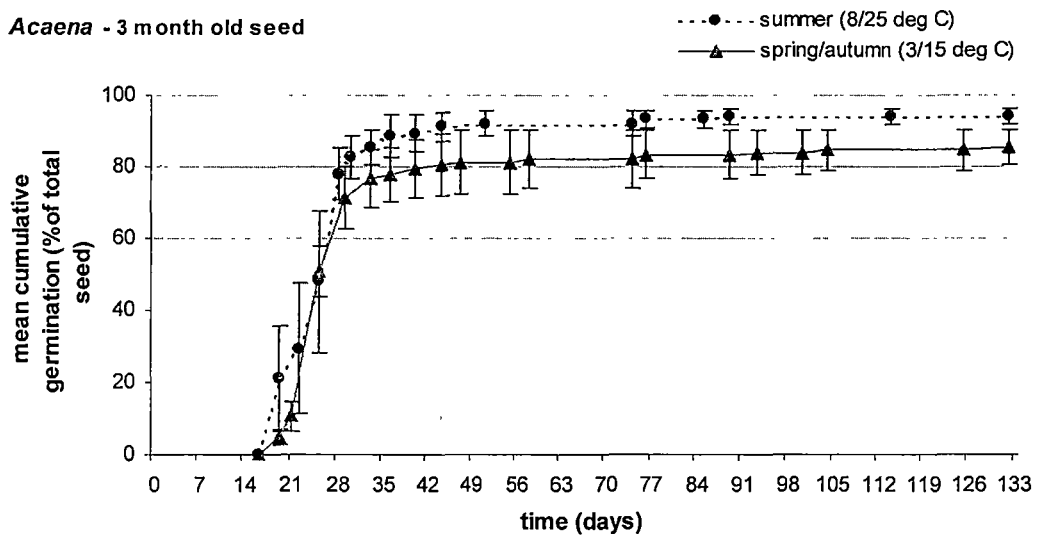


Figure 6.2 *Aceana novae-zelandiae* **germination curves in two temperature regimes. Values shown are means ±SE.**

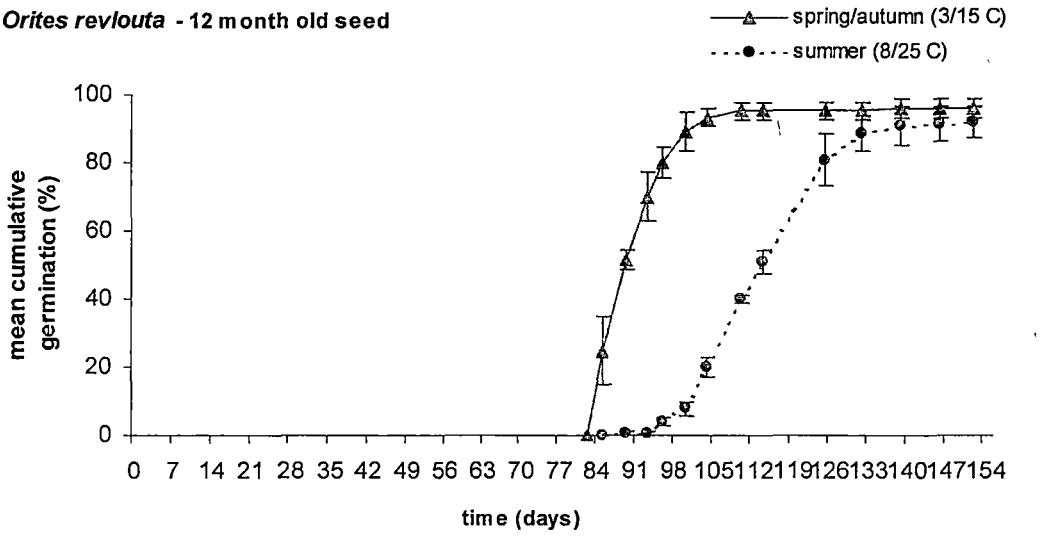


Figure 6.3 *Orites revoluta* **germination curves in two temperature regimes. Values shown are means ±SE.**

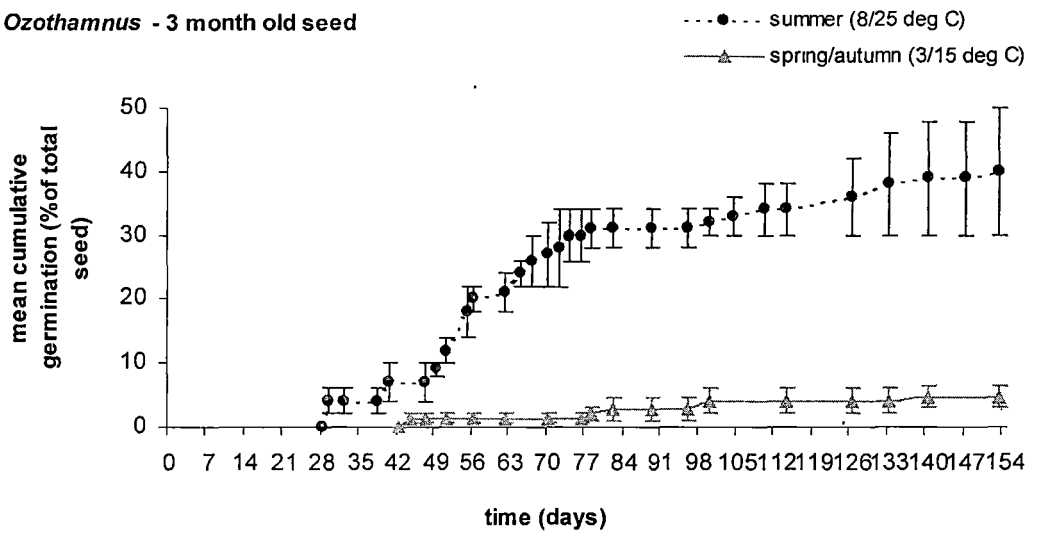


Figure 6.4 ***Ozothamnus hookerii*** **germination curves in two temperature regimes. Values shown are means ±SE.**

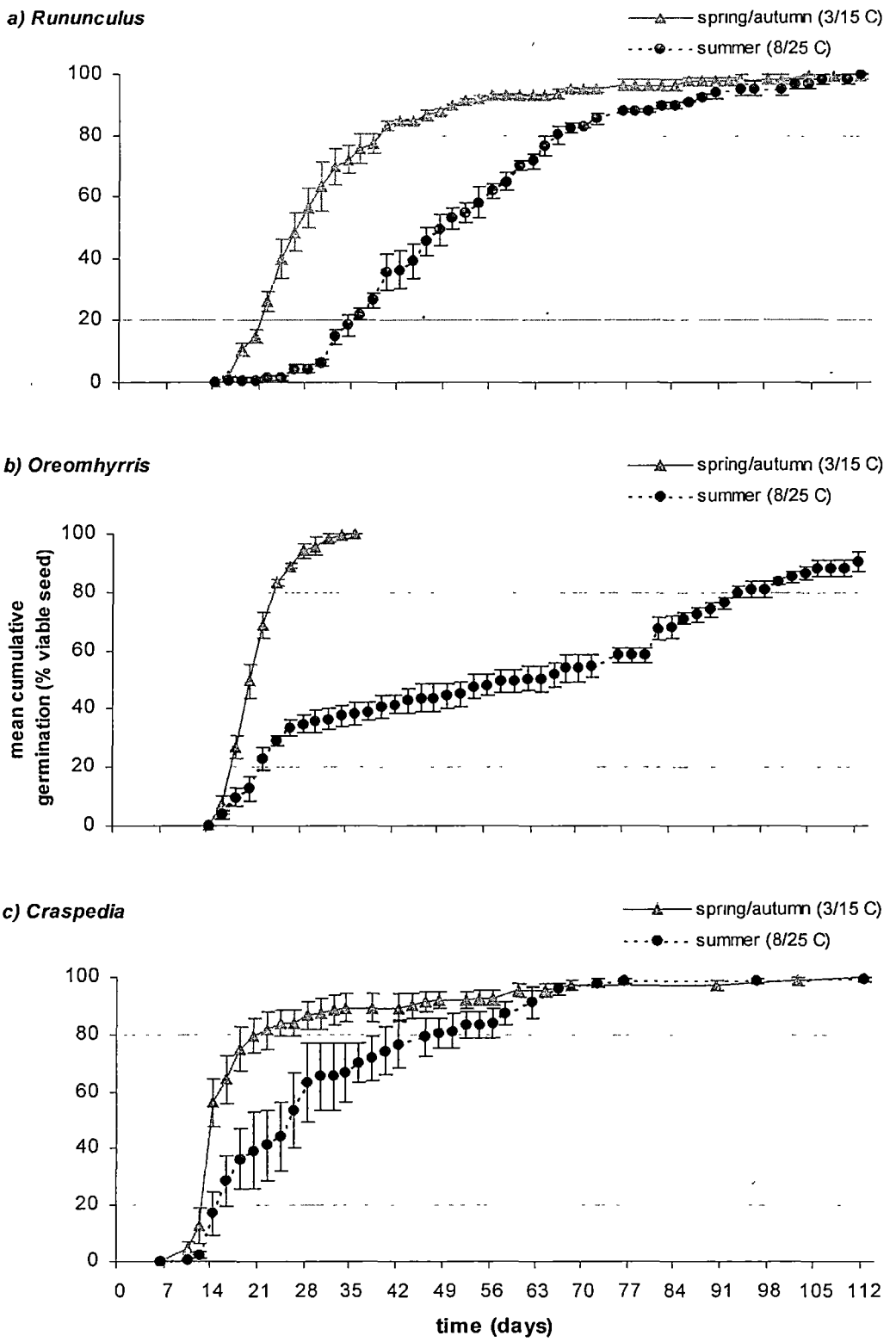


Figure 6.5 Germination curves of a) *Ranunculus pascuinus*, b) *Oreomhyrris ciliata* and c) *Craspedia coolaminica* in two temperature regimes. Values shown are means ±SE.

Time to commencement of germination varied from 10 (*C. coolaminica*) to 89 days (*O.revoluta*) (Figure 6.6), and the rate of germination for the first 7 or 8 days was higher in the spring/autumn treatment for most species (Figure 6.7). Mean number of days taken to reach 50% germination varied from 13.7± 0.7 (*C. coolaminica*), to 113.3± 4.1 (*O. revoluta*) (Figure 6.8). *Oreomhyrris ciliata* ($F_{1,4}$=19.33, P=0.01), *R. pascuinus* ($F_{1,4}$=41.88, P=0.003), and *O. revoluta* ($F_{1,4,}$=54.23, P=0.002) took significantly longer to reach 50% germination under "summer" conditions than under the "spring/autumn" regime (Figure 6.8). *Craspedia coolaminica* had a higher germination rate for the first 8 days in the cooler conditions ($F_{1,4}$=10.92, P=0.03), but subsequently the time taken to reach 50 % germination was not significantly different between the treatments. No significant differences between the two temperature regimes were observed in 3 month old *A. novae-zelandiae* seeds for any of the four properties measured. No calculations were performed for *O. hookeri* due to its low germination.

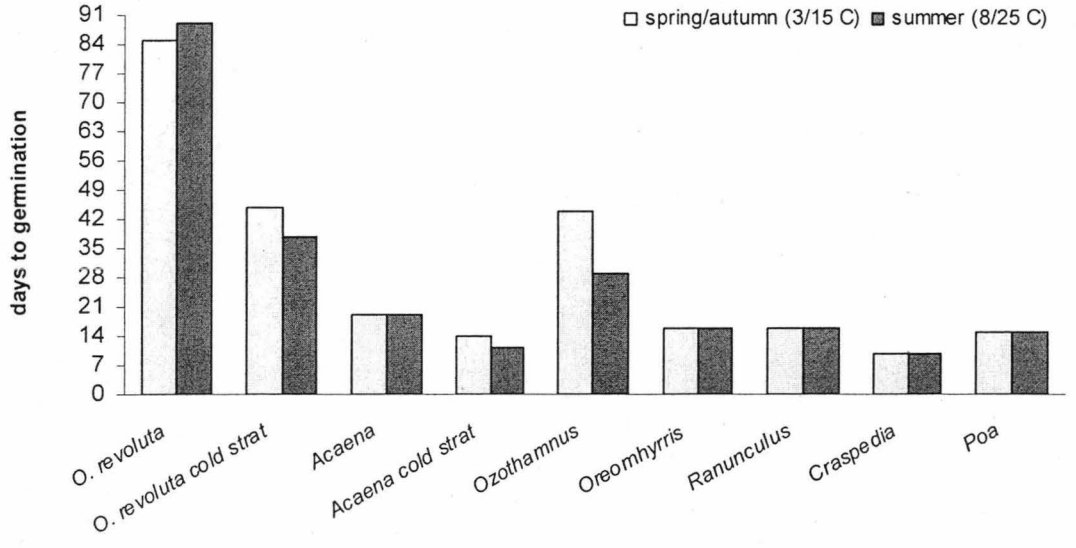


Figure 6.6 Time to commencement of germination in both temperature regimes.

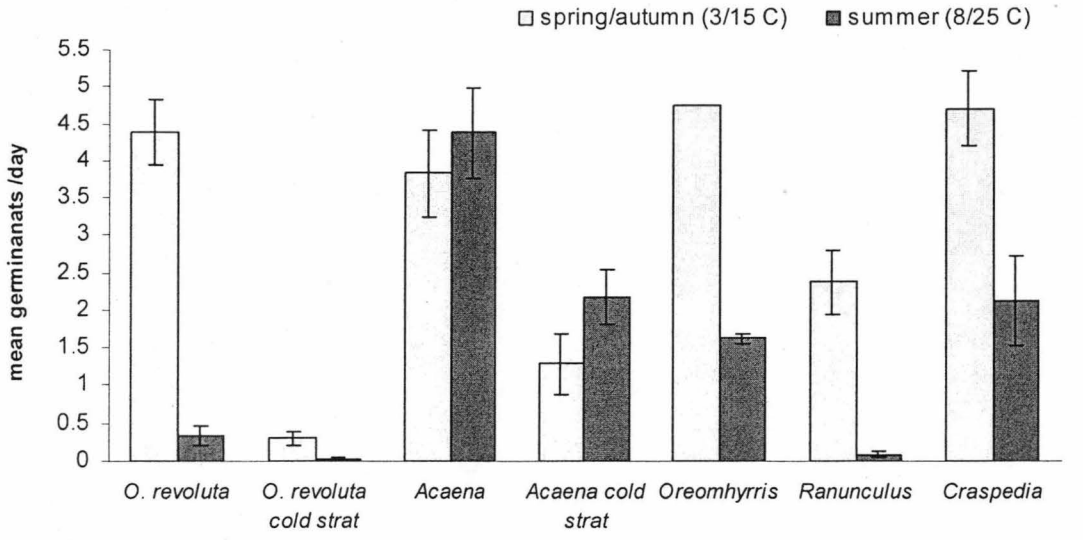


Figure 6.7 Average daily germination rate during first week in two temperature treatments. Bars are ±SE.

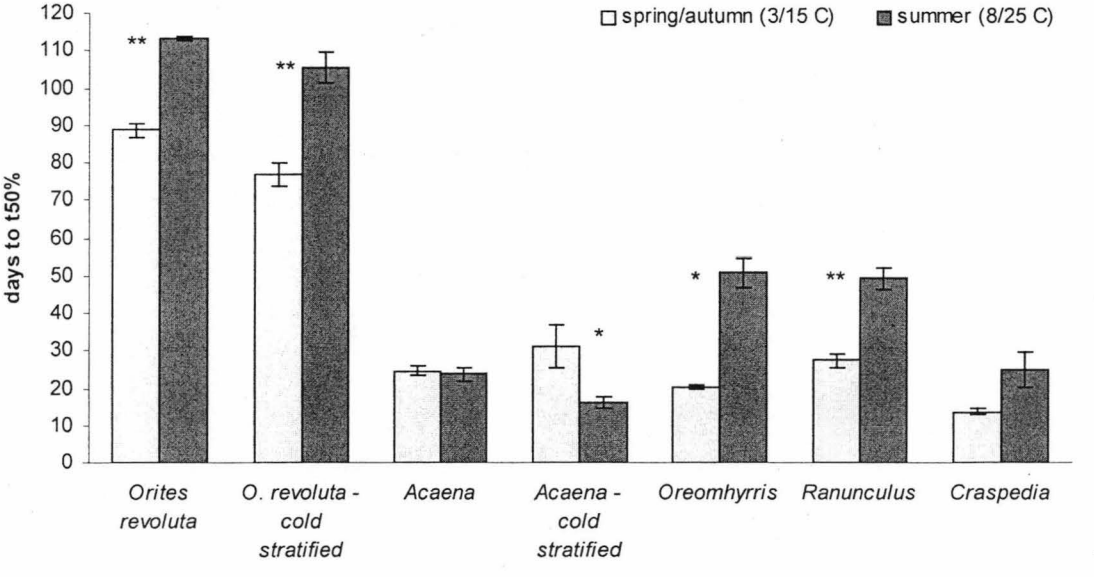


Figure 6.8 Mean time taken to 50% maximum germination ±SE * indicates differences between the two temperature regimes at P<0.05, ** indicates P<0.01.

Cold stratification and alternating temperature regimes

Unlike the 12 month old *O. revoluta* seeds, one month old cold stratified *O. revoluta* seeds showed significantly higher mean germination under the cold treatment (82.7 ±2.4 %), than in warm conditions (56 ±7.9 %, $F_{1,8}$=10.36, P=0.01) (Figure 6.9). Final germination percentages of cold stratified A. *novae-zelandiae* on the other hand were not significantly different between temperature regimes (Figure 6.10).

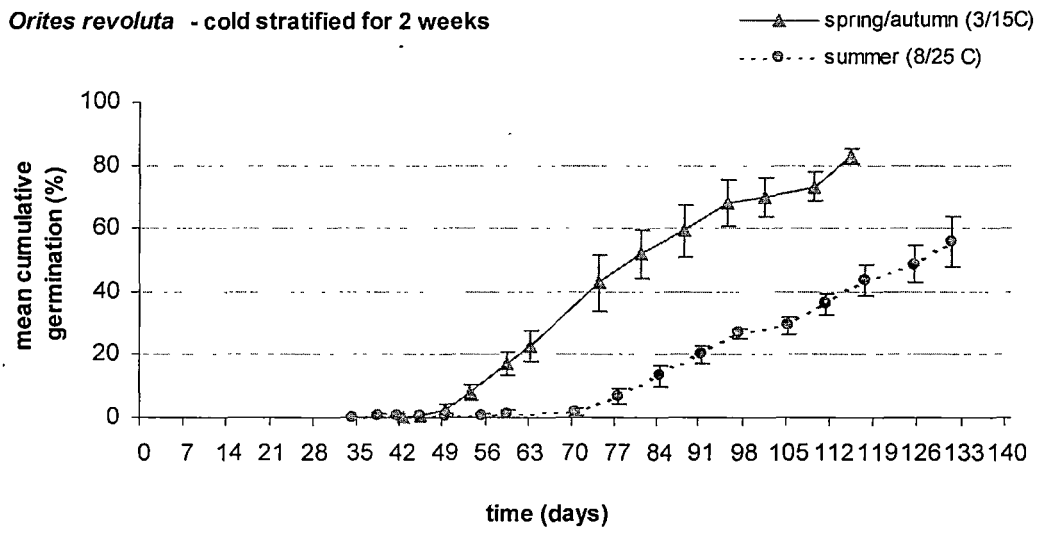


Figure 6.9 Mean cumulative germination of cold stratified 1 month old seed of *Orites revoluta* in two temperature regimes. Values shown are means ±SE.

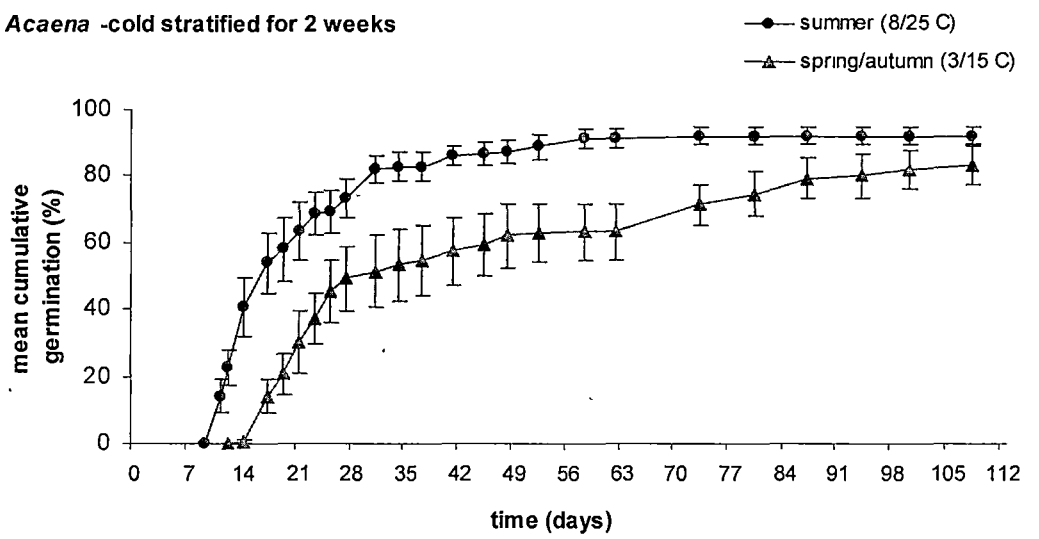


Figure 6.10 Mean cumulative germination of cold stratified 4 month old seed of *Acaena novae-zelandiae* in two temperature regimes. Values shown are means ±SE.

Cold stratified *O. revlouta* took significantly longer ($F_{1,7}$=21.24, P=0.003) to reach 50% germination under "summer" conditions than under the "spring/autumn" regime (Figure 6.8). In contrast, cold stratified *A. novae-zelandiae* seeds responded positively to the warmer temperatures ($F_{1,8}$=7.96, P=0.02), although the germination rate was not significantly different for the first 8 days ($F_{1,8}$=2.77, P=0.13) (Figure 6.7).

Effect of pre-treatments on G. australis and O. acicularis

None of the additional treatments applied to seeds of *G. australis* and *O. acicularis* improved germination rates in these two species. Both the one month old and the 25 month old *Grevillea* seed did not respond to smoke, heat, or the combination of the two, with germination virtually 0% after nine months of incubation, including two months after seed coat abrasion for the two year old seeds. *Orites acicularis* seeds did not respond to smoke or heat either, in light or dark conditions, with or without eight weeks of cold stratification, with germination in all treatments, including controls, below 5% after five months of incubation. However, when at the conclusion of the experiment *O.*

acicularis seeds were removed from the growth cabinets and placed on a lab bench, they continued germinating at a slow rate for another seven months. At that time, most replicates reached less than 30% germination, with many seeds eventually lost to fungal invasion, making viability difficult to determine.

DISCUSSION

Germination responses to the two temperature regimes varied between species. Six of the ten species tested germinated readily to over 80%, regardless of the temperature treatment. The warm temperature regime promoted germination in only one species, *Ozothamnus hookerii,* but even under those conditions the final mean germination was just 40%. In contrast, incubation in the cold treatment promoted germination in one month old *Orites revoluta* seed, although this effect could potentially be removed with longer trial time. Three species, *Grevillea australis, Geranium sessiflorum* and *Orites acicularis* had very poor germinability under all treatments.

Oreomhyrris ciliata, Craspedia coolaminica and *Ranunculus pascuinus* germinated readily, taking less than four weeks to reach 50% germination in the spring/autumn treatment. This was significantly sooner than the seeds in the summer treatment (except for *C. coolaminica,* which was highly variable), and was due to the initial higher germination rate in the cold regime for these three species. The synchronous germination of relatively fresh seed under lower temperatures suggests an autumn crop of seedlings coinciding with increasing April rainfall on the Plateau (see Table 1.1), with very few seeds, if any, persevering in the seed bank until spring. As discussed in Chapter 3, masses of seedlings were observed germinating in gaps in April. This pattern of autumnal germination to escape summer drought and take advantage of reliable rainfall has also been observed for many temperate grassland species (Morgan 1998, 2001). The predominance of seedling mortality reported for some alpine sites during the

growing season, rather than in winter, suggests that seedlings are more vulnerable to summer drought rather than to severe winter conditions even in such limiting environments (Urbanska & Schuetz 1986; Forbis 2003). A few individuals are likely to start germinating late in the summer if moisture conditions are favourable, but the extended germination period under higher temperatures suggests there will still be a large proportion of ungerminated seeds when the autumn rains arrive. Seedling densities observed in the field (Chapter 3) did not reveal a strong seasonal pattern however, suggesting that a variety of germination patterns is likely to be occurring *in situ*, although a more frequent seedling census time might reveal otherwise.

Cooler temperatures also accelerated and synchronised the germination phase in *Orites revoluta*. However, time taken to commencement of germination, and hence to 50% germination under both temperature regimes was considerably longer than for any other species. The initial germination rate was also very low in cold stratified *O. revoluta* under both temperature regimes, reflecting the extended germination period. No loss of viability after 12 months of seed storage, the long time to commencement of germination, and the lengthy germination period of fresh seed indicates that this species most likely overwinters until spring following dispersal in late autumn, or even persists in the seed bank until the following autumn.

Acaena novae-zelandiae also germinated readily in both cold and warm temperature regimes. Yet in contrast to the previous four species, there was no difference in the initial germination rate between the two temperature treatments. Four month old, cold stratified seeds however, reached 50% germination sooner in the warm treatment, indicating that the germination rate eventually increased under "summer" conditions. Therefore, given sufficient moisture, this species is likely to germinate just as readily in summer, spring or autumn. Although able to germinate in summer, the interaction of moisture and temperature requirements is likely to limit the majority of seedling emergence to spring and autumn. In a study of four subalpine *Acaena* species from New Zealand, seeds predominantly germinated in a temperature range of 14-21°C, but with water potentials ranging from only 0 to –0.2 MPa (Conner 1987). The ability to take

advantage of high temperatures and germinate late in summer or early in autumn if moisture conditions are favourable, might give seedlings a better chance of establishment before winter. Shimono & Kudo (2003) observed this to be the case in fellfield populations of *Potentilla matsumurae* in the Taisetsu Mountains of northern Japan. Seedlings that emerged in August had a higher survivorship than those that emerged in June or July, due to drought and unpredictable frost early in the season, but early emerging seedlings had greater survivorship over winter, due to having achieved a larger size prior to the onset of winter.

Very low temperatures did not prevent germination of fresh *Acaena novae-zelandiae* seeds from coastal Britain, with 90% germination after 25 days at a constant temperature of 15°C, and 20% germination after 80 days at 5°C (Gynn & Richards 1985). If *A. novae-zelandiae* is capable of germinating at such low temperatures on the Central Plateau, and given that most *Poa gunnii* seeds germinated at 4°C in under two weeks, some seeds of these two species are likely to germinate very late in the autumn, in winter, or very early in spring, taking advantage of the wetter conditions at those times of the year (see Chapter 2). The wide range of germination temperatures, and lack of dormancy indicates opportunistic germination influenced more by moisture than temperature. This means that very few seeds will be incorporated into the seed bank during winter to recruit the following spring, although *P. gunnii* seeds, like many other Australian grasses (see references in Bell 1999) might need a period of post ripening over winter. This ongoing, non-specialized germination strategy has also been observed in many native species recruiting in perennial *Themeda triandra* grassland communities in south-eastern Australia (Morgan 2001).

Cold stratifying *P. gunnii, A. novae-zelandiae* and *O. revoluta* seeds for longer than two weeks could have helped determine if spring or autumn germination was more probable, with spring germinating seeds usually responding to a period of chilling, while inducing dormancy in autumn germinators in temperate species (Masuda & Washitani 1992; Shimono & Washitani 2004). Baskin & Baskin (1998) recommend up to 12 weeks of cold stratification, but three to four weeks is often adequate. Subjecting seeds to

refrigeration for only two weeks might not have been sufficient to replicate winter conditions and affect germination, but it did not induce dormancy either, suggesting that spring germination is likely. Cold stratification hastened the onset of germination in *O. revoluta* (approximately five weeks cf. 12 in non stratified seeds), but it is not possible to separate the moist chilling pre-treatment effect from the effect of seed age. This is also a problem in interpreting the results for *A. novae-zelandiae* where four month old, cold stratified seeds reached 50% germination sooner in "summer" than in "spring", while non-stratified, three month old seed showed no difference between treatments.

Ozothamnus hookerii was the only species where final germination was much higher in the warm treatment than in the cold treatment, and therefore recruitment is more likely to occur very soon after dispersal, with no large overwintering seed bank. Unless the seedlings are robust enough to withstand periods of drought, germination of this shrub might be restricted predominantly to summers with higher than average rainfall, with very poor recruitment during drier years. The relatively low germination of this species even under a warm regime could be due to loss of seed viability after several months of storage.

Grevillea australis was one of two species that did not germinate successfully from fresh or previous seasons' seed, under either temperature regime and with or without a short period of cold stratification, or after smoke and heat was applied. Heat and smoke treatments simulating fire conditions have been very successful at promoting germination in a range of species, including a number of *Grevillea* species, often having a synergistic effect (Dixon *et al.* 1995; Edwards & Whelan 1995; Roche *et al.* 1997; Bell 1999; Kenny 2000; Morris 2000; Pickup *et al.* 2003). Even in species without obvious need of fire, such as lettuce (Drewes *et al.* 1995) and celery (Thomas & van Staden 1995) germination was improved by smoke. Some species of *Grevillea* are also known to respond to scarification even though the seed coat is permeable to water, indicating that dormancy mechanisms are largely controlled by the seed coat, rather than the embryo or any changes of metabolic activity due to heat (Edwards & Whelan 1995; Morris 2000; Morris *et al.* 2000; Pickup *et al.* 2003). Mechanical disruption of the seed

coat is therefore needed before germination can proceed in the majority of seeds. Heating *G. australis* seeds to 80°C for 10 minutes was not sufficient to crack the seed coat, the mechanism by which dormancy was broken in *G. barklyana* (Edwards & Whelan 1995), but temperatures of 110-120°C were lethal to seeds of six *Grevillea* species tested by Auld & Tozer (1995). Many *Grevillea* species appear to have a proportion of non dormant seeds, however, which varies considerably between species (Edwards & Whelan 1995; Pickup *et al.* 2003). *Grevillea buxifolia* and *G. speciosa* (collected at maturity) showed high germinability after 10 min of exposure to temperatures between 40 and 100°C (Auld & Tozer 1995), while around 20% of fresh *G. macronulata* and *G. speciosa* seeds (Morris 2000), and 18% of *G. barklyana* (Edwards & Whelan 1995) and 36% of *G. rivularis* soil-stored seed (but not fresh seeds) (Pickup *et al.* 2003) maintained at room temperature responded to moist conditions alone, not requiring any pre-treatment. This ability of some species to germinate from fresh seed is possibly due to differences in seed coat characteristics. Rapid uptake and loss of water has been documented for seven east Australian *Grevillea* species (Morris 2000; Morris *et al.* 2000), indicating fluctuating soil moisture levels could contribute to post dispersal weathering of the seed coat, and release from dormancy over time. Yet even when the seed coat of the two year old seeds was eventually abraded, it did not improve germination after two months. In contrast, some Australian and South African members of the Proteaceae have been reported to germinate readily to within 100% between 18 to 40 days after sowing with no specialised dormancy breaking requirements (Stock *et al.* 1990), presumably from fresh seed.

Seed coat hardness is also likely to have been responsible for preventing germination in *Geranium sessiflorum*. However unlike in *Grevillea*, Baskin & Baskin (1974) found that in freshly matured seeds of *Geranium carolinianum* the hard coats are impermeable and will not imbibe water unless scarified. The embryos are also conditionally dormant, needing a short period (1.5 months) of after-ripening to become nondormant, allowing this winter annual to delay germination until autumn and thus avoid summer droughts. Yet even nonscarified seeds of *G. carolinianum* germinated to around 50% at alternating 15/6°C after 3.5 months of storage (Baskin & Baskin 1974).

Although *O. acicularis* seed is similar to *O. revoluta*, and the two species co-occur on the Central Plateau, *Orites revoluta* has been reported to readily recover from rootstock following fires, and more slowly from seed, whereas *O. acicularis* does not return and tends to be replaced by *Ozothamnus hookeri* and *Olearia algida* (Corbett 1996). The pre treatments applied in this study confirm lack of response to heat and smoke. After six months in a growth cabinet, the highest germination in any replicate of 1.5 month old *O. acicularis* seed was 4%. However, following removal from growth cabinets, the seeds continued germinating for several months on a lab bench. This species is therefore likely to have a higher, more restricted germination temperature range, or another dormancy breaking requirement not fulfilled in this study, with fire being an unlikely cue. Higher incubation temperatures could be also beneficial to *G. australis*. Haselhurst (1977) reported that germination in *Grevillea banksii* was depressed by night temperatures below 15°C, so the night temperatures of 8 and 3°C trialed here could have been too low to promote germination in both species.

The high germinability under wide temperature regimes for most species observed in this study suggests that many forb and grass species in the area have the potential to recruit readily and opportunistically if moisture requirements are met, making them likely colonisers of available habitat almost throughout the year. The rapid and synchronous germination of *Oreomhyrris ciliata, Craspedia coolaminica, Rununculus pascuinus* and *Poa gunnii* under low temperatures indicates a preference for autumn recruitment to avoid summer drought, leaving very few seeds to be incorporated into an overwintering seed bank. *Grevillea australis* and *Orites acicularis* however, two important, dominant shrubs in the Central Plateau area, appear to have a large proportion of dormant seeds, which do not germinate under the temperature scenarios conducive for herbs. There are no published reports on their germination requirements, and unlike many other members of the Proteacea, including several Australian *Grevillea* species, neither *G. australis* nor *O. acicularis* responded to heat or smoke treatments in this study. The potential requirements of higher night-time temperatures and, in *G. australis*, seed coat weathering to break dormancy, would limit these shrubs to a window of

summer recruitment from an overwintering seedbank, possibly extending over more than one season.

Chapter 7. General Discussion and Management Implications

The process of revegetation in alpine areas is exceedingly slow, especially if reliant exclusively, or for the most part, on re-establishment from seedlings in the absence of vegetatively propagating species. Loss of vegetation often goes hand in hand with soil degradation or loss. In the case of Tasmania's Central Plateau Region, vast sheet erosion of areas above 1 000 m a.s.l. has completely removed the O and A soil horizons, resulting in a particularly challenging environment for plant re-establishment. The severity of the growing conditions has often been cited as the reason behind the limited revegetation taking place despite the cessation of burning and grazing two decades ago. However, aside from anecdotal observations, there are no published studies describing the microclimatic environment experienced at the seedling level, which can be expected to be very variable in such a structurally heterogenous landscape. This study aimed to investigate potential limits to regeneration by assessing not only the physical microenvironment at the soil surface (Chapter 2), but also by examining other possible biotic factors affecting seedling recruitment (Chapters 4-6).

Seedlings were present on the Plateau at all sites and at all times of the year that censuses were carried out. Even in gaps, seedling numbers were comparable to those that colonized a primary successional landscape on the Pumice Plains of Mount St. Helens (Titus & del Moral 1998), and higher than emergence in gaps in sub-arctic heath (Welling & Laine 2002). There was a distinct pattern of clumping of seedlings under *Grevillea australis* shrubs compared to gaps, and this relationship was independent of season at all sites. This could be because one or a combination of the following is occurring:

1. More seeds arrive or accumulate under *Grevillea* canopies,
2. More seeds germinate under *Grevillea* canopies,

3. Seedling survivorship is greater under *Grevillea* canopies.

The fate of seeds in the community was thought to be of particular importance, given previous research suggesting the crucial role of seed distribution in vegetation dynamics (Fenner 1992; Nakashizuka *et al.* 1993; Scherff *et al.* 1994; Aguiar & Sala 1997; Welling 2002). Aguiar and Sala (1997) predicted that in the Patagonian Steppe, most recruitment will take place in microsites that contain established plants, due to the large number of seeds these patches accumulate during secondary seed dispersal. In order to determine the importance of seed distribution to recolonisation patterns in the present study, community seed dispersal was investigated using seed traps located in diverse microhabitats, including under *Grevillea* shrubs and in denuded patches (Chapter 4). Although more seeds were trapped in gaps (11 835.4 ±2 928.8 seeds m^{-2}) than under *Grevillea* canopies (4 641.4 ±1 017.1 seeds m^{-2}) at all sites during the study period, the difference was not significant due to the high variability between traps. The total number of taxa captured during the sampling period did not differ between bare (5.2 ±0.2 taxa/trap) and *Grevillea* (3.9 ±0.2 taxa/trap) microhabitats either, nor was there a distinct suite of species associated with microhabitat type. Small-seeded wind dispersed shrubs, such as members of the Epacridaceae and Asteraceae, dominated the seed rain numerically at the two shrubby heath sites (Carter Lakes and Lake Botsford), while Poaceae and Asteraceae seeds were prevalent at the grassy heath site (Liawenee Exclosures), where the seed rain was also rich in grasses and herbaceous species taxonomically. Overall, there was an ample supply of seed and a variety of species dispersing to all microhabitats throughout the year, so low seed deposition was not responsible for lower seedling numbers in gaps.

As this was a community-wide seed rain study, it is difficult to compare the results to others where one or two species are singled out for investigation, and consequently conflicting conclusions are reached depending on seed characteristics of the study species (Fuentes *et al.* 1984; Aguiar & Sala 1997; Russell & Schupp 1998; Bullock & Moy 2004). On the other hand, the most numerically abundant species in the seed rain can bias the results for the whole community, while not necessarily being an important

species in the landscape or in terms of recolonisation potential. While it appears that in general, *Grevillea australis* canopies did not necessarily provide a more favourable site for seed arrival and retention overall, *Grevillea* seeds were more likely to be trapped in Edge microhabitats than anywhere else. This could have important implications for revegetation patterns of gaps. If higher seed numbers lead to greater germination of *Grevillea* in a "safe site" which is also favourable for establishment, this could have positive consequences for gap closure, even if seeds of most other species are distributed differently. Nevertheless, the consensus in the literature appears to be that shrubs accumulate seeds of many species either during primary or secondary dispersal or both, and interpreting which stage plays a more significant role in this process will be affected by seed trap design. Separating the primary and secondary phase of dispersal in a windy environment like the Central Plateau is difficult regardless of trap design. The funnel seed traps used here potentially underestimated secondary dispersal, and overestimated trapping in microtopographically featureless, smooth, sandy bare patches.

In terms of seed removal, only invertebrates were assessed as potential harvesters (Chapter 5). Although exclusively seed eating species were found to be absent from the area, ground dwelling invertebrates, including omnivorous *Iridomyrmex* ant species, were active in both open and closed microhabitats during summer and autumn. *Iridomyrmex* spp. were numerically dominant in pitfall traps at Lake Botsford, while *Anonychomyrma* sp. were co-dominant at Carter Lakes. Ants are important post dispersal seed predators in most Australian systems (Andersen 1982; Andersen & Ashton 1985; Andersen 1991) but their role in Tasmanian or mainland Australian alpine areas has not been investigated, based on the assumption that these groups are absent from high altitude environments. Recently, however, ants have been shown to remove over 20% of seeds of dwarf shrub and woody cushion species, and on average 10% of all species tested in the central Chilean Andes at 2700 m elevation (Muñoz & Cavieres 2006). The findings of Muñoz and Cavieres (2006) suggest that the role of invertebrates, especially ants, in post-dispersal seed predation deserves to be investigated further in alpine systems.

Data on the next step in the revegetation process, i.e. the suitability of gaps versus closed microhabitats for germination is absent from this study. In order to track recruitment, frequent visits would be necessary to the sites, involving tagging of individual seedlings. This was not feasible logistically as part of this study, and is possibly a major deficiency in gaining an accurate and detailed picture of the regeneration process. However, laboratory seed germination trials attempted to partially fill this gap. Most species tested germinated readily, with temperature having no effect, or gemination occurring sooner in spring/autumn temperature regimes than in summer treatments. Only *Grevillea australis* and *Orites acicularis* did not germinate successfully under any conditions. Although it is likely that many herbaceous species will germinate rapidly (in under three weeks) both in gaps and under *Grevillea* canopies in spring or autumn while there is more reliable rainfall, the two dominant shrub species will probably have an overwintering seed bank and will emerge over a longer period. Seedlings of both species were present throughout the year, with numbers of both higher under *Grevillea* canopies. Given the substantial seed input for most of the year, and the ready germination of the species tested, recruitment for many species could be expected to be high. Rapid and prolific germination could be followed by high mortality but missed between distant seedling census dates. Abundant recruitment of Asteraceae species was in fact observed in gaps outside census dates, which was not reflected in subsequent counts. Seed germination could be even higher in gaps than in closed microhabitats, but is likely to be relatively sporadic given the consistently higher seedling densities under *Grevillea*.

The apparent high mortality of seedlings in gaps, and the evidence of higher seedling numbers under *Grevillea* canopies therefore point to greater survivorship in closed microhabitats compared to bare patches. Although there is general agreement that the shelter provided by nurse plants, be they shrubs or cushion plants or even microtopographic features like rocks, is due to their ameliorating effect on the microclimate, quantitative data on the parameters responsible for the ameliorating effect are sparse, as are data on the degree of climate amelioration. No doubt this is partly because microclimatic techniques have become commonly accessible only relatively

recently, and some background knowledge of the field is desirable in order to gather meaningful data. The potentially intensive maintenance regime of loggers and sensors could also be a deterrent in less accessible areas. The microclimatic differences between the major microhabitats in the present study - large bare gaps and under *Grevillea australis* canopies - were described in terms of relative humidity, daily minimum temperature, solar radiation at the soil surface, and wind speed at 10 cm above ground. Contrary to expectations, there were no clear differences in relative humidity, or average daily minimum temperatures between the two microhabitats. However, higher wind speed and solar radiation were confirmed in gaps, as well as greater frequency and extent of frost heave, despite the frequency and intensity of freeze-thaw cycles being similar between the two microhabitats.

Frost heave is primarily controlled by soil moisture (Outcalt 1971; Matsuoka 1996), a feature of the physical environment that was not quantified in this study. Although surface relative humidity is similar in gaps and under *Grevillea* canopies (or possibly higher under *Grevillea*), subsurface moisture is likely to be greater in gaps, away from root systems and transpiring plants, which often are also situated higher than eroded bare patches. Competition for water under existing vegetation has often been cited to counter-balance the facilitation provided by nurse plants (Franco & Nobel 1988; Aguiar *et al.* 1992). Although the root system environment of seedlings under *Grevillea* canopies could be drier than subsurface conditions in gaps, this advantage would in turn be negated by increased frost heave in bare patches, the most significant threat to seedling survival on the Plateau. Substantial frost heave (exceeding 25 mm) was documented in gaps at all study sites, regardless of elevation or differences in soil characteristics. The most severe events occurred in winter, following the main germination period in autumn and decimating the emerged seedlings. Mortality of seedlings due to frost heave and needle ice has been reported from alpine and subalpine areas world wide (Gradwell 1960; Brink 1964; Leigh *et al.* 1987; Castro *et al.* 2004), as well as polar desert (Anderson & Bliss 1998).

While daily minimum temperatures appeared not to be buffered by *Grevillea* canopies, the combination of low temperatures and elevated solar radiation in gaps could lead to photoinhibition damage and consequently seedling mortality. Furthermore, increased seedling survivorship under canopies might be influenced more by maximum daily temperatures causing heat stress in bare microhabitats. Although this could be a major factor tipping the balance against seedlings in the open, obtaining reliable, continuous data for this parameter has proven difficult, and was omitted from analysis, but cannot be excluded from consideration. Seedling mortality in gaps has often been attributed to drought experienced in exposed microhabitats (Rey & Alcántara 2000; Castro *et al.* 2004), but given the similar daily minimum relative humidity between gaps and *Grevillea*, higher maximum temperatures at the surface could be of more consequence in summer.

One of the most striking observations of the microclimate data, was the variation recorded by replicate sensors in each microhabitat, so it is possible that the averages used for comparison obscured the very real differences between microsites within each microhabitat, which are not themselves homogenous. There might exist a critical threshold of replicates that sample these microsites in order to screen out the noise at the microhabitat scale. *Grevillea* canopies might provide favourable as well as unfavourable microsites for recruitment, and it is the relative proportions of those compared to gaps that result in greater seedling survival. Differences in temperature and relative humidity between gaps and sheltered microhabitats could also be more unambiguous at higher elevations than measured in the current study (1050 m a.s.l.).

It is evident that some aspects of the microclimate at the soil surface restrict seedling survival in alpine heath communities despite adequate seed input and successful germination. Although Williams and Ashton (1987; 1988) and Williams (1992) reported shrub seedling establishment (including *Grevillea australis*) in gaps up to 1 m^2, on the Central Plateau, substantial soil loss has occurred and stony soil remnants in the gaps might present a more challenging environment for establishment. The lack of

organic horizons in the soil profile could also hinder seed bank formation for some species reliant on protracted recruitment.

The degraded shrubby alpine vegetation on the Central Plateau presents a very limited regeneration niche for seedlings of all species. Those that can perhaps withstand some degree of competition from facilitator shrubs such as *Grevillea australis,* or are less reliant on them for establishment, could drive the change in community composition and succession in the future.

IMPLICATIONS FOR MANAGEMENT

This study highlights the need to limit disturbance in alpine environments, and for ongoing rehabilitation in areas that have been disturbed. Information regarding natural regeneration can help prioritise restoration efforts and limit trial and error. Active restoration on the Plateau needs to focus on providing safe sites that favour seedling survival following seed dispersal. Exogenous seed input will not necessarily speed up the process of revegetation without suitable microhabitats for establishment, as the heath communities do not appear to be seed limited in bare areas in most need of cover. Using advanced *Grevillea australis* plants as a revegetation species in areas where it is common might provide a longer term source of safe sites for colonisers. As the shrubs senesce and open up, the balance between ameliorating conditions for seedling survival could tip towards more favourable conditions for establishment and growth under the shrub's canopy. Although both jute matting and *Orites acicularis* slash reduced frost heave and the frequency of freeze-thaw events compared to bare areas, planting of *Grevillea* juveniles (or a similar prostrate species) could be more visually acceptable and perhaps more cost effective. However, the susceptibility of *Grevillea australis* to trampling reinforces the need to exclude stock, restrict horseriding and 4Wdriving activities, and educate bush walkers about the fragile nature of some of the communities.

SUGGESTIONS FOR FUTURE RESEARCH

This study identified numerous gaps in knowledge regarding natural revegetation processes in degraded areas on the Central Plateau. The general picture presented here needs to be narrowed down in terms of seed rain and soil seed bank, seedling dynamics and seed predation. A more intensive study of seed dispersal patterns of selected species, and examination of seed accumulation in the soil will give insight into future community composition and change. The identity of colonisers needs to be examined, and individuals need to be monitored to gauge rates of mortality and *in situ* patterns of germination. Comprehensive multi species seed baiting studies targeting both vertebrate and invertebrate species are also needed. There is also a lot of room to clarify microclimatic differences between gaps and closed microhabitats, or artificial ground covers. Physical and chemical properties of soils, including nutrient status could be compared given the large nature of eroded patches and other research pointing to existing nurse plants as nutrient islands in alpine and arid systems (Franco & Nobel 1989; Uesaka & Tsuyuzaki 2004). This work could be extended to include other degraded communities on the Plateau, and take the impact of herbivory into account. Most importantly these questions need to be approached as long term studies that address the seasonal variability evident here.

This study has examined many aspects of the problem of plant regeneration in a degraded landscape and provided important ecological baseline data as well as future direction for conservation and management of large areas of the Tasmanian Central Plateau.

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